# THE MUTANTS OF THE EXTREME LEFT END OF THE SECOND CHROMOSOME OF *DROSOPHILA MELANOGASTER*

CURT STERN[1]
*Kaiser Wilhelm Institut für Biologie, Berlin*
AND
CALVIN B. BRIDGES
*Carnegie Institution of Washington, and Columbia University*

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TABLE OF CONTENTS

| | PAGE |
|---|---|
| INTRODUCTION | 504 |
| PART I | 504 |
| Star | 504 |
| Reappearances of star | 506 |
| Telegraph | 508 |
| Telegraph by star backcross | 508 |
| Telegraph black stock | 509 |
| Aristaless | 510 |
| Aristaless by star backcross | 510 |
| Aristaless$^2$ | 511 |
| Dachsous | 511 |
| Dachsous black backcross | 512 |
| Dachsous black purple by lobe$^2$ backcross | 512 |
| Dachsous$^2$ | 513 |
| Dachsous$^3$ | 513 |
| Dachsous$^3$ by star backcross | 513 |
| Expanded | 515 |
| Expanded by star backcross | 515 |
| PART II | 516 |
| Telegraph by star backcross | 516 |
| Aristaless by star backcross | 517 |
| Dachsous by star backcross | 518 |
| Expanded by star backcross | 518 |
| Telegraph expanded double recessive | 519 |
| Telegraph dachsous double recessive | 521 |
| Telegraph star by dachsous backcross | 521 |
| Aristaless dachsous double recessive | 522 |
| Aristaless star by dachsous backcross | 522 |
| Aristaless expanded double recessive | 523 |
| Aristaless star by expanded backcross | 523 |
| Expanded dachsous double recessive | 524 |
| Expanded star by dachsous backcross | 525 |
| The order of the loci | 526 |
| Aristaless dumpy by star backcross | 527 |
| Construction of Map | 527 |
| SUMMARY AND EVALUATION OF THE MUTANTS | 529 |
| LITERATURE CITED | 530 |

[1] Fellow of the International Education Board, resident at COLUMBIA UNIVERSITY, New York City.

## INTRODUCTION

The number of mutant characters known in *Drosophila melanogaster* is continually increasing. Many of the new mutants have no special interest in themselves, but they may serve as tools for the investigation of other problems. Before they can be used with certainty, their general characteristics and linkage relations must be determined.

The important dominant mutant star had been located at the extreme left end of the map of the second chromosome. Four recessive mutants had been found that are very closely linked to star. An account of star, by BRIDGES and MORGAN, has appeared in Carnegie Publication No. 278, pages 259–273. References to the others, namely, telegraph, aristaless, dachsous and expanded, have appeared in several maps and publications, notably "The Genetics of Drosophila," Bibliographica Genetica, 2 : 1–262. The present paper gives, in Part I, descriptions of these mutants and an account of the older data collected by BRIDGES, and, in Part II, the more precise determinations of the locations made recently by STERN. The map based on these determinations is given as figure 1.

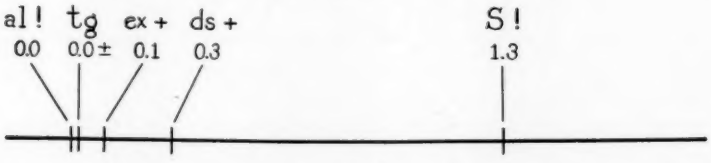


FIGURE 1.—Map of the extreme left end of chromosome II of *Drosophila melanogaster*. This map is based on the data of table 21. The symbol (!) denotes the most useful mutants, (+) those nearly as good, while the absence of a mark indicates that the mutant is important only in special connections.

## PART I

### *Star*

The mutant star, found by BRIDGES, February 12, 1915, has been probably the most useful mutant in the second chromosome. This was due primarily to its dominance, its excellent viability (roughly 98 percent that of the wild type) and its very favorable location, since it was the mutant farthest to the left among those whose linkage relations were approximately known. The separation of star from the wild type is not as easy or as rapid as desirable, and hence considerable experience in its use is necessary before the classification is reliable in a critical case.

The character star, as seen under a low power of the binocular (about 12 diameters) differs from the wild type in that the eyes are (1) rougher in

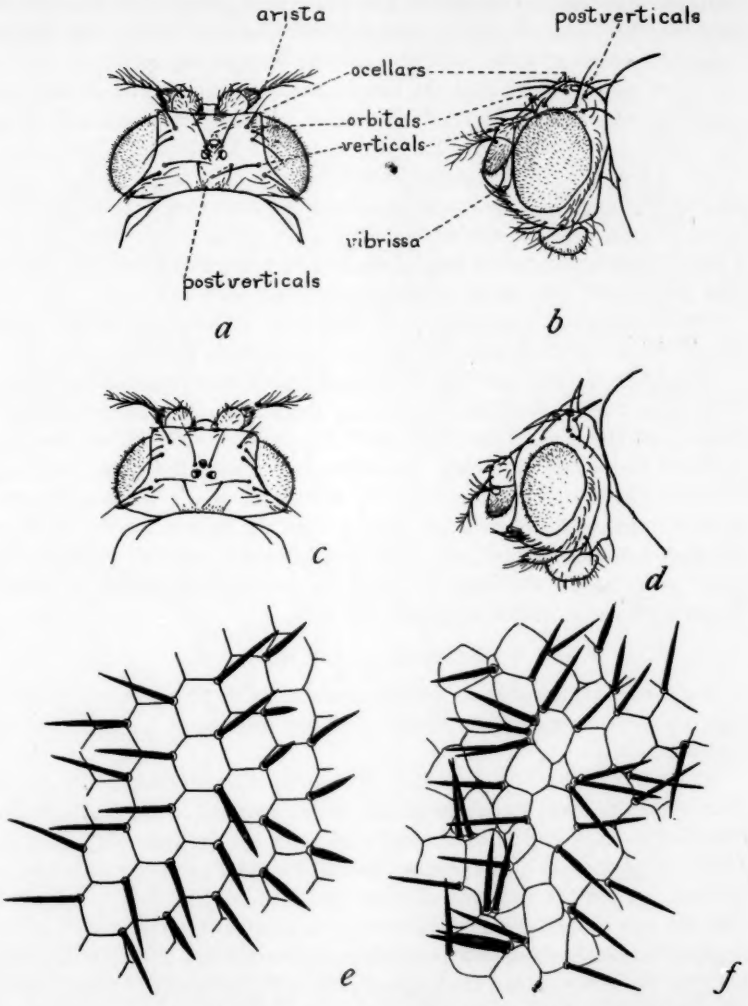


FIGURE 2.—*a* and *b*, top and side views of head of wild-type individual of *Drosophila melanogaster*, with nomenclature of bristles. *c* and *d*, top and side views of the head of the mutant star. *e*, enlarged view of facets and eye-hairs of a wild-type individual (regularity of direction of eye-hairs disturbed by pressure of coverglass). *f*, enlarged view of facets and eye-hairs of the mutant star. (Irregularity in direction of eye-hairs is normal to star.)

texture, (2) somewhat smaller in size, (3) slightly narrower in the anteroposterior direction, (4) slightly darker in color, and (5) faintly scintillating with tiny points of light. (Compare figure 2c with 2a, and 2d with 2b.) A higher power shows that the roughness in texture is due to the ommatidia being arranged irregularly instead of in regular rows, and being of varying size, shape and color (compare figure 2f with 2e). The scintillation is due to reflection of light from the tiny hairs between the facets. In the wild-type eye the hairs stand singly in a perfectly regular latticework pattern and are radially directed. In the star eye the hairs are missing from some spaces and aggregated in two's and three's in others, and point in all directions. (Compare figure 2f with 2e.)

The homozygous condition of the star gene is invariably lethal. The character as described is the heterozygous dominant form.

Since the mutant star had more favorable characteristics, especially with respect to its dominance, than the other mutants of the group at the left end of the map, it has been made the point of reference in locating mutants in its neighborhood. For this same reason the data involving star and the mutants throughout the remainder of the chromosome are greater in amount and better in quality than the data in which the other leftmost mutants are involved. This difference will probably continue for some years and accordingly the locus of star will maintain its prime importance in the region to the left of black.

## Reappearances of star

Star, or an allelomorph so similar as not to be distinguished by inspection or in the course of experimentation, has reappeared by mutation on four occasions:

(1) In a cross between two stocks involving only sex-linked characters (cut female by eosin miniature garnet[2] male) BRIDGES found that half the offspring in one pair culture showed a star-like eye (culture 8718, June 8, 1918). Examination of the original stocks showed no star-like individuals present, nor did the pedigrees of those stocks involve star. Tests showed that the new character was a heterozygous dominant, lethal when homozygous, located in chromosome II, and much to the left of black. Crosses between the new star and the original gave in $F_1$ the typical 2 star : 1 wild type ratio (8756,8757; total 262 star : 132 wild type).

(2) MOHR found star again (July 20, 1920) and has reported the facts for this case (MOHR 1923).

(3) The third reappearance of star occurred in the spring of 1925 in the cultures of L. V. MORGAN. Allelomorphism was established by

the fact that a cross between a stock of the new star balanced by curly (WARD 1922) and a stock of the original star balanced by curly gave in $F_1$ only flies that were both star and curly, exactly as though either star had been bred to itself in balanced stock. (Unpublished data of L. V. MORGAN.)

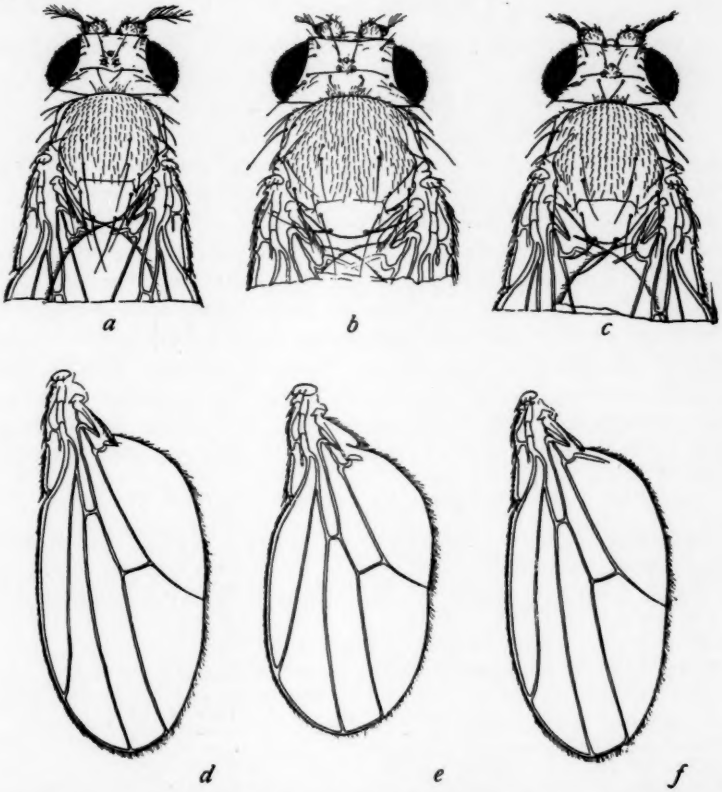


FIGURE 3.—*a* and *d*, dorsal view of head and thorax and a wing of a wild-type individual of *Drosophila melanogaster*. *b*, the mutant aristaless, showing reduced aristae and posterior bristles on the scutellum widely separated and strongly divergent. *c*, the mutant telegraph, showing the slight erection of the posterior bristles of the scutellum. *f*, the wing of the mutant telegraph, showing weak spots in the second longitudinal vein. *e*, the wing of the mutant dachsous, showing the crossveins close together.

(4) In a cross involving the second-chromosome dominant curly Doctor HELEN REDFIELD found one curly female with an eye like star.

The character was found to be dominant and due to a gene in the curly-bearing second chromosome. In crosses to the original star it was found that the new star was lethal in the compounds with the old star, and hence must be an allelomorph of star. (Unpublished data of Doctor H. REDFIELD.)

### *Telegraph*

In establishing a pure stock of the third-chromosome recessive smudge, BRIDGES found a culture (No. 3947, March 27, 1916), in which a majority of the flies showed a break or weak space in the second longitudinal vein (Compare figure 3f with 3d). Many of the flies showed more than one such break, and from this dot-and-dash appearance of the vein the mutant was called telegraph. When telegraph males and females were bred together most of the progeny showed the character. This indicated that the mutant was a recessive for which the stock was homozygous but that the character overlapped the wild type. In some individuals telegraph failed to show, and in others could only be distinguished with difficulty in one wing. Later it was found that many of the telegraph flies showed another characteristic, namely, the posterior scutellar bristles were more or less erect, as in vestigial, instead of pointing backward. (Compare figure 3c with 3a.) This bristle characteristic could often be used as an index of the mutant in those flies in which the breaks were absent or weak.

### Telegraph by star backcross

Telegraph males were crossed to star females, and in $F_1$ the telegraph character was found to be recessive. The $F_1$ star flies were inbred in pairs for an $F_2$ generation (table 1). The telegraph character reappeared in

TABLE 1

*$P_1$, telegraph ♂×star ♀; $F_1$ star ♀×$F_1$ star ♂.*

| MAY, 1917 | TELEGRAPH | STAR | TELEGRAPH STAR | WILD TYPE |
|---|---|---|---|---|
| 7203 | 86 | 220 | 1 | 1 |
| 7204 | 80 | 194 | 3 | 1 |
| 7205 | 105 | 210 | .. | .. |
| Total | 271 | 624 | 4 | 2 |

slightly less than the expected frequency. Only four of the $F_2$ flies showed both star and telegraph, while 271 showed simply telegraph. This strong linkage showed that the locus of telegraph is in the second chromosome, and also that it is very close to that of star. Only two flies that were not-

star failed to show telegraph. These were probably due to crossing over rather than to overlapping of the telegraph character. The percentage of recombination was calculated from the average of the two recombination classes, as compared with the original combination class telegraph

$$\left(\frac{3}{271+3}\times 100=1.1\right)$$

The star class could not be used in the calculation since it was complex, including recombinations as well as original combinations.

From the star class of table 1 virgin females were mated to telegraph males for backcross counts (table 2). Some difficulty in classification was

TABLE 2

*Telegraph over star* ♀ *(from table 1)*×*telegraph* ♂.

| MAY, 1917 | TELEGRAPH | STAR | TELE-GRAPH STAR | WILD TYPE | CONTINUED | TELEGRAPH | STAR | TELE-GRAPH STAR | WILD TYPE |
|---|---|---|---|---|---|---|---|---|---|
| 7249 | 107 | 105 | 2 | 2 | 7323 | 29 | 35 | 1 | 2 |
| 7250 | 63 | 63 | 1 | 1 | 7648 | 161 | 134 | .. | 7 |
| 7251 | 49 | 49 | .. | 5 | 7649 | 142 | 161 | .. | 8 |
| 7252 | 215 | 208 | 1 | 4 | 7654 | 78 | 79 | .. | 2 |
| 7268 | 92 | 89 | .. | 4 | | | | | |
| | | | | | Total | 936 | 923 | 5 | 35 |

encountered, and the class marked wild type (+) was composed partly of true recombinations due to crossing over but mostly of overlaps from the genotypically telegraph class. The percentage of recombination was at first calculated from the total flies of tables 1 and 2 as 2.0, and in the maps prepared (see especially the maps in BRIDGES 1921 and in MORGAN, BRIDGES and STURTEVANT 1925) the telegraph star distance was given as 2.0. Because the phenotypic class wild type was partly due to overlaps the calculations should have been made on the basis of the telegraph flies alone, and would then have been 0.7

$$\left(\frac{9}{1216}\times 100=0.7\right)$$

Telegraph black stock

A female showing both telegraph and star (from table 2) was crossed to a black male. $F_1$ heterozygous star females were crossed to telegraph males (culture 7383, telegraph star = 71, wild type = 79, telegraph = 2, star = 1). Both of the recombinational telegraph males that occurred were crossed to black of unrelated stock. Half of the offspring were black. These black flies were inbred and in the next generation somewhat

less than a quarter of the flies showed telegraph as well as black. These latter were inbred to give a telegraph black stock. The fact that the above procedure was successful in giving a telegraph black stock made it seem probable that the locus of telegraph is to the left of star rather than to the right. If it were to the right, the telegraph flies tested must have resulted from the less frequent double crossing over. A three-point backcross involving telegraph star and black was undertaken to test this point, but difficulties in classification prevented it from being conclusive.

As will be shown in a later section of this paper, the work of STERN has shown that the locus of telegraph is indeed to the left of that of star, and that the distance between them is about 1.3 units.

### *Aristaless*

In examining an $F_2$ culture (8028, November 7, 1917) involving eosin, vermilion, forked and a new mutant "disbanded" that had arisen in the California wild stock, BRIDGES found that approximately a quarter of the flies showed posterior scutellar bristles that were erect, diverged strongly, and were widely separated from each other (Compare figure 3b with 3a). A pure stock of this recessive was established and freed of the other mutant characters originally present. It was then found that the flies that showed "repelled" bristles were further characterized by great reduction or even complete absence of the aristae (figure 3b). It was anticipated that this mutant, called aristaless, would be especially valuable since it affected a region of the body affected by few other mutants and hence could be used widely without confusion in classification.

### Aristaless by star backcross

Aristaless was crossed to star dichaete, and several $F_2$ cultures were raised. Aristaless occurred freely in the dichaete $F_2$ flies but apparently not at all in the star $F_2$ flies. From this it was concluded that the locus of aristaless is in the second chromosome, and also that it is very close to that of star.

From the $F_2$ flies, star females and aristaless males were bred together for backcross counts (table 3). In two of the cultures the viability of aristaless was very low, but in the other two it was normal. There were three recombinations in a total of 334 flies, or 0.9 percent of recombination.

Since at that time work on the third-chromosome mutants was being carried on practically to the exclusion of other work, as soon as the above data were obtained the mutant was turned into stock without further testing. In making the earlier maps of the second chromosome the

locus was put down as to the right of star, since the probability that any mutant should lie to the left of star was thought to be less than that it should be to the right. The recent tests of STERN (see below) have shown that the locus of aristaless is in reality to the left of that of star, and that the distance between them is roughly 1.0 units.

TABLE 3

*$F_2$ aristaless over star ♀ × $F_2$ aristaless ♂.*

| DECEMBER, 1918 | ARISTALESS | STAR | ARISTALESS STAR | WILD TYPE |
|---|---|---|---|---|
| 9029 | 10 | 47 | .. | .. |
| 9187 | 19 | 59 | 1 | 2 |
| 9198 | 43 | 43 | .. | .. |
| 9263 | 50 | 60 | .. | .. |
| Total | 122 | 209 | 1 | 2 |

### *Aristaless²*

In looking over the second-chromosome stock "fringed," STERN found several flies of both sexes with reduced aristae and erected posterior scutellar bristles (January 1926). Fringed was kept as a balanced stock over curly. The fact that all flies exhibiting the new mutant were fringed not-curly indicated that its locus was in the not-curly second-chromosome. This, together with its characteristics, made it probable that one was dealing with an allelomorph of aristaless. By crossing the mutant flies to aristaless and obtaining only aristaless-like flies in the $F_1$ generation, the allelomorphism was proven. Aristaless² is a somewhat less extreme character than the old aristaless, both in regard to the reduction of the aristae and the erection of the scutellar bristles. The classification is as easy as in aristaless. If viability tests should show a better viability of aristaless² than of aristaless, then the former would replace the old allelomorph in future work.

### *Dachsous*

In a mixed stock of black and black purple (Culture 9068, November 12, 1917), BRIDGES noticed that a small percentage of the flies had wings which were shorter than normal and in which the crossveins were very close together (figure 3e). The abdomen and legs were also shorter, and the general appearance of the fly was similar to that of the mutant dachs. The "dachsous" flies were inbred, and they produced only dachsous offspring, which showed that the character was a recessive. A dachsous black stock and a dachsous black purple stock were isolated.

### Dachsous black backcross

Three cultures of a dachsous black backcross were raised (table 4). They gave respectively 22, 25 and 27 percent of recombination for dachsous and black. This linkage ratio showed that the locus of dachsous is in the second chromosome.

TABLE 4

*$P_1$, dachsous black×wild type; BC., $F_1$ wild type ♀×dachsous black ♂.*

| OCTOBER, 1920 | DACHSOUS BLACK | WILD TYPE | DACHSOUS | BLACK |
|---|---|---|---|---|
| 12055 | 104 | 118 | 26 | 36 |
| 12056 | 86 | 85 | 26 | 32 |
| 12061 | 116 | 118 | 40 | 45 |
| Total | 306 | 321 | 92 | 113 |

### Dachsous black purple by lobe² backcross

Dachsous black purple males were crossed to females with the dominant character lobe², whose locus is at 70 in the second chromosome (BRIDGES 1921). In the backcross cultures (table 5) the percentage of recombination for dachsous and black was 36.4, for dachsous and purple 38.9 and for dachsous and lobe² 41.0. That is, the locus of dachsous is farthest from that of lobe and hence is to the left of black. When the locus of dachsous was first calculated on the basis of the data of tables 4 and 5, proper allowance was not made for double crossing over and the locus was entered as probably 12 units to the right of star (see MORGAN, BRIDGES and STURTEVANT 1925, page 92).

TABLE 5

*$P_1$, dachsous black purple ♂×lobe² ♀; BC., $F_1$ lobe² ♀×dachsous black purple ♂.*

| NOVEMBER 1920 | DACHSOUS BLACK PURPLE | | DACHSOUS BLACK PURPLE LOBE² | | DACHSOUS BLACK PURPLE LOBE² | | DACHSOUS BLACK PURPLE LOBE² WILD TYPE | | DACHSOUS BLACK PURPLE LOBE² | | DACHSOUS BLACK PURPLE LOBE² | | DACHSOUS BLACK PURPLE LOBE² | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 12147 | 98 | 98 | 71 | 49 | 5 | 7 | 21 | 13 | 1 | .. | 9 | 9 | 3 | .. | .. | .. |
| 12154 | 104 | 115 | 54 | 71 | 4 | 4 | 18 | 12 | .. | .. | 11 | 9 | .. | 1 | 1 | .. |
| 12155 | 75 | 114 | 53 | 51 | 4 | 1 | 15 | 14 | 1 | .. | 5 | 10 | 1 | 3 | .. | 2 |
| 12256 | 95 | 100 | 59 | 59 | 10 | 3 | 17 | 18 | 1 | 2 | 14 | 15 | 3 | 1 | .. | .. |
| 12157 | 72 | 92 | 42 | 49 | 3 | 3 | 9 | 10 | 4 | .. | 7 | 9 | .. | 2 | .. | .. |
| Total | 444 | 519 | 279 | 279 | 26 | 18 | 80 | 67 | 7 | 2 | 46 | 52 | 7 | 7 | 1 | 2 |

Dachsous was given to MOHR for use in studying the relationships of the supposed deficiency "gull," and MOHR reported by letter that he

found that dachsous and star gave about 1 percent of recombination. The tests of STERN (see below) have shown that the locus of dachsous is to the left of star by about 1.0 unit.

### *Dachsous*$^2$

The stock of speck was found by BRIDGES to be homozygous for a character that resembled dachsous, (April 2, 1925). Crosses between this mutant and dachsous gave only flies like dachsous. In dachsous$^2$ the crossveins are as close together as in dachsous, but the wings, legs, and body are only slightly shortened.

### *Dachsous*$^3$

In a stock of wild flies collected by Doctor D. E. LANCEFIELD at Olympia, Washington, in the summer of 1925, BRIDGES found several males and females that had crossveins very close together (November 5, 1925). Such flies reappeared continuously in several generations, usually late in the course of the culture. Attempts to breed them together failed. Likewise females used in outcrosses produced no offspring. Four such females, that were fully ten days old, were dissected and it was found that two of them contained no ovaries. The oviducts were present and a small tuft of trachae where the ovaries are normally situated. One female differed in that one partly developed egg was present. The fourth had five such eggs. Of these, four stuck out radially from the tuft of trachae and broke away easily. The other egg was partly within the oviduct, wrong end foremost. Of approximately twenty females used in crosses none gave offspring. The males proved fertile and a self-perpetuating stock was obtained by crossing them to curly, and then inbreeding the curly $F_1$ flies. The fact that the $F_2$ flies in this stock were all of two classes, simple curly and those with close-crossveins but not-curly, showed that the locus of the mutant is in the second chromosome.

### Dachsous$^3$ by star backcross

A backcross with star gave less than one percent of recombination (table 6). Crosses of close-crossvein to dachsous gave only flies with close-crossveins. Accordingly the new mutant is an allelomorph of dachsous and is called dachsous$^3$. The compound between the two allelomorphs dachsous and dachsous$^3$ had wings nearly as long as dachsous$^3$, abdomen occasionally shortened but not so strikingly as in dachsous. The viability and fertility of the compound were apparently normal.

In viability dachsous$^3$ was very poor, 50 percent that of star in table 6, while dachsous has always been excellent (99 percent that of wild type).

TABLE 6

*$P_1$, dachsous$^3$×star; BC., $F_1$ star ♀×dachsous$^3$ ♂.*

| DECEMBER 1925 | DACHSOUS$^2$ | STAR | DACHSOUS$^3$ STAR | WILD TYPE |
|---|---|---|---|---|
| 15233 | 53 | 96 | .. | 1 |
| 15236 | 77 | 167 | 1 | 1 |
| Total | 130 | 263 | 1 | 2 |

Dachsous$^3$ was delayed in emergence; few dachsous$^3$ flies appeared until the not-dachsous$^3$ flies had been hatching for five days. The first dachsous$^3$ flies to emerge had no bristles on the scutellum, or around the ocelli, and the scutellum was shortened. The wings were spread slightly and often lacked the anterior crossveins. The flies that hatched later had normal head and scutellum and there were even one or two extra bristles on the scutellum. The wings and abdomen of dachsous$^3$ were not shortened as much as those of dachsous or dachsous$^2$.

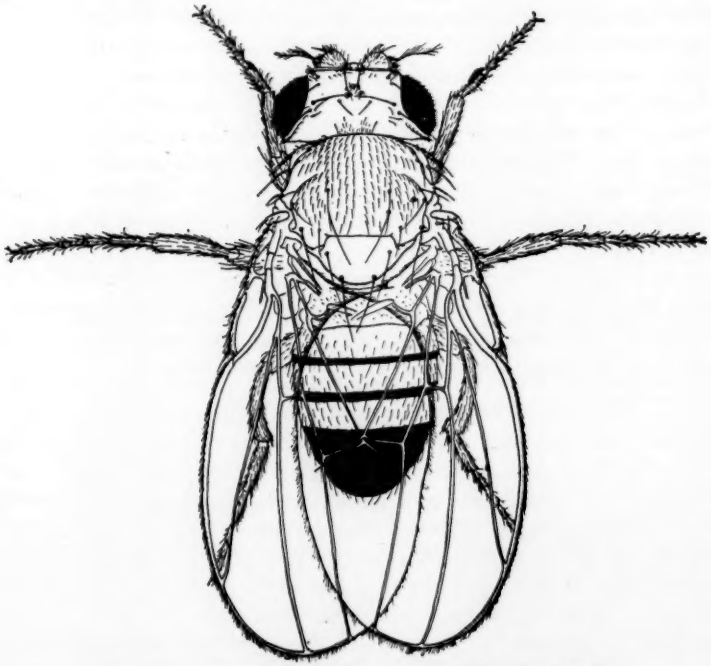

FIGURE 4.—The mutant expanded, showing large, broad wings.

### *Expanded*

In determining the locus of the sex-linked lethal, lethal 15, BRIDGES found that one culture (8118, November 21, 1917), was giving a few flies with wings very broad, and similar in posture to curved, namely, extended rather widely at the sides and held above the back, except that a curvature of the wing brought the tips of the wings down to the normal level (figure 4). The crossveins were also closer together than normal. The eyes were somewhat reduced and roughish in texture. The flies were larger than normal.

#### Expanded by star backcross

"Expanded" males were out-crossed to star dichaete females, and in $F_1$ gave only not-expanded progeny, from which the character was known to be recessive. $F_1$ star dichaete females were crossed to expanded males that had been secured by breeding together expanded males and females from the original culture (table 7).

TABLE 7

*$P_1$, expanded ♂ × star (D) ♀; BC., $F_1$ star (D) ♀ × expanded ♂.*

| NOVEMBER 1917 | EXPANDED | STAR | EXPANDED STAR | WILD TYPE |
|---|---|---|---|---|
| 8250 | 70 | 80 | 3 | 9 |
| 8295 | 44 | 52 | .. | 8 |
| 8365 | 219 | 237 | 2 | 4 |
| 8391 | 150 | 157 | 16 | 2 |
| 8393 | 134 | 149 | 6 | 4 |
| Total | 617 | 675 | 27 | 27 |

The different cultures gave contradictory results. The individuals classified as recombinations were probably mostly errors due to unfamiliarity with the character and to confusion between the roughish eye of expanded, and the roughish eye of star. The apparent percentage of recombination was 4.0, and accordingly the locus of expanded was set down tentatively as about 4 units to the right of star.

STERN (see below) found that the reduction in the eye of expanded tends to increase as the cultures become older; while on the other hand the wing character becomes less extreme in older cultures. Trustworthy classifications could be made for expanded and star after familiarity with the interaction of the two had been acquired. The locus was found by STERN to be about 1.2 units distant from star, and to be to the left, not to the right.

PART II

Preliminary tests of BRIDGES, reported in Part I, had shown that the dominant character star and the four recessive characters telegraph, aristaless, expanded, and dachsous form a group of genes at the left end of the map of the second chromosome. There still remained to be determined, first, the sequence of the loci of these genes within the group, this being the most important and constant feature represented by a chromosome map, and second, the relative distances between the loci.

The first step in the procedure was to find more exactly, by a series of two-point backcross experiments, on a fairly large scale, the distance of each of the recessives from the locus of star, which, on account of its dominance, was the easiest point of reference.

Thus, the general procedure in the first series of tests was to cross star to a given recessive, and then to mate several of the $F_1$ star double heterozygous females

$$\frac{r \quad +^s}{+^r \quad S}$$

each to a male of the recessive stock. Since star is a dominant, the male of the recessive stock is in effect a double recessive

$$\frac{r \quad +^s}{r \quad +^s}.$$

The results of the series of distance tests should eliminate certain sequences of loci as improbable and limit the number of subsequent tests.

*Telegraph by star backcross*

On inspection of the telegraph stock it was seen that about half of the flies failed to show any break in the longitudinal vein. And in the telegraph by star backcross results this same overlap was observed. In calculating recombination percentages for cases in which one of the mutant characters overlaps wild type, fairly correct values may be obtained by disregarding all flies that fail to show the character in question and using only those flies in which the character was seen. This method was followed in Part I in calculating the telegraph star recombination percent.

However, in the $F_1$ of the telegraph by star cross it was seen that about 6 percent of the flies heterozygous for telegraph showed breaks in the longitudinal veins. In the backcross results the flies in which the breaks were due to dominance of the character could not be distinguished

from the flies in which the breaks were the homozygous recessive form. Consequently the calculations could not be made on the basis of the flies that showed the break. It was found that the other characteristic of the telegraph mutant, namely, erected scutellar bristles, was strictly recessive and accordingly in making the classifications telegraph flies were identified solely by use of this index. The erect-bristle character also overlapped the wild type by about 50 percent and in making the calculations all not-erected flies have been disregarded. The fifteen cultures (table 8) produced a total of 1169 flies with erected bristles, of which 11, or 0.9 percent were star and were therefore recombinations due to crossing over between the loci of telegraph and star.

TABLE 8

*$P_1$, telegraph ♀ × star ♂; BC., $F_1$ star ♀ × telegraph ♂ (Jan. 1925).*

| TELEGRAPH | TELEGRAPH STAR | TELEGRAPH | TELEGRAPH STAR | TELEGRAPH | TELEGRAPH STAR | TELEGRAPH | TELEGRAPH STAR |
|---|---|---|---|---|---|---|---|
| 56 | .. | 95 | .. | 98 | 1 | 43 | 1 |
| 49 | .. | 70 | 1 | 56 | .. | 99 | .. |
| 41 | 1 | 70 | 1 | 97 | .. | 134 | 3 |
| 85 | 1 | 68 | 2 | 97 | .. | | |
| | | | | | | 1158 | 11 |

*Aristaless by star backcross*

The character aristaless, like telegraph, has two prominant characteristics, namely, the aristae are reduced or even absent, and the posterior scutellar bristles are erected, strongly divergent and situated abnormally far apart. It was found that the arista character, though fluctuating in the amount of reduction, is a safe index of the homozygous recessive character. But the scutellar bristles character was occasionally

TABLE 9

*$P_1$, aristaless ♀ × star ♂; BC., $F_1$ star ♀ × aristaless ♂. (Jan. 1925).*

| ARISTALESS | STAR | ARISTALESS STAR | WILD TYPE | ARISTALESS | STAR | ARISTALESS STAR | WILD TYPE |
|---|---|---|---|---|---|---|---|
| 118 | 131 | .. | 1 | 64 | 67 | 1 | .. |
| 61 | 57 | 3 | 2 | 131 | 173 | 3 | 1 |
| 73 | 87 | 1 | 1 | 149 | 157 | 4 | 1 |
| 69 | 119 | .. | .. | 61 | 72 | .. | 1 |
| 120 | 120 | 2 | 1 | 99 | 108 | 1 | 1 |
| 115 | 126 | 4 | 1 | 124 | 136 | 3 | 2 |
| 85 | 110 | 1 | 2 | 18 | 32 | 1 | 1 |
| 148 | 154 | 2 | 1 | 37 | 34 | 2 | .. |
| 166 | 168 | 1 | 4 | 188 | 176 | 1 | 2 |
| 53 | 64 | 2 | 2 | | | | |
| 156 | 162 | 1 | 1 | 2035 | 2244 | 33 | 25 |

apparent in heterozygous flies, and in homozygous flies was sometimes difficult to distinguish. The classification throughout has been on the basis of the arista characteristic of "aristaless."

Two sets of backcross cultures (table 9; 1, the first seven cultures and 2, the remainder) were raised, and these agreed in the percentages of recombination (1.4 and 1.3). The total number of recombinations in the two sets was 58 in a total of 4337 flies, or 1.3 percent.

### *Dachsous by star backcross*

The new dachsous by star backcross (table 10) gave a total of 4269 flies of which 31, or 0.7 percent, were recombinations.

TABLE 10

*$P_1$, dachsous ♀ × star ♂; BC., $F_1$ star ♀ × dachsous ♂. (Jan. 1925).*

| DACHSOUS | STAR | DACHSOUS STAR | WILD TYPE | DACHSOUS | STAR | DACHSOUS STAR | WILD TYPE |
|---|---|---|---|---|---|---|---|
| 173 | 175 | 1 | 4 | 170 | 166 | 2 | 2 |
| 159 | 174 | .. | 1 | 190 | 205 | .. | 2 |
| 96 | 123 | 1 | 3 | 225 | 209 | 2 | 3 |
| 156 | 163 | 1 | 1 | 203 | 219 | 1 | 1 |
| 193 | 176 | .. | 1 | 130 | 161 | 2 | .. |
| 157 | 144 | .. | 1 | | | | |
| 235 | 236 | 1 | 1 | 2087 | 2151 | 11 | 20 |

### *Expanded by star backcross*

The new expanded by star backcross (table 11) gave a total of 3060 flies, of which 46, or 1.5 percent, were recombinations.

TABLE 11

*$P_1$, expanded ♀ × star ♂; BC., $F_1$ star ♀ × expanded ♂. (Jan. 1925).*

| EXPANDED | STAR | EXPANDED STAR | WILD TYPE | EXPANDED | STAR | EXPANDED STAR | WILD TYPE |
|---|---|---|---|---|---|---|---|
| 149 | 118 | 1 | 3 | 190 | 179 | 4 | 1 |
| 153 | 138 | 6 | 2 | 297 | 238 | 5 | 5 |
| 169 | 169 | 2 | 1 | 206 | 204 | 2 | 1 |
| 162 | 173 | 2 | 5 | 148 | 191 | 2 | 2 |
| 68 | 62 | 1 | 1 | | | | |
| | | | | 1542 | 1472 | 25 | 21 |

The results of the above tests with star confirmed the earlier finding of BRIDGES that the loci of the five mutants lie very close together (table 12). The loci were found to be even closer together than expected. No certain conclusion as to the relative distances could be drawn, since the

probable errors of such small percentages are high, and the possible effects of linkage modifications in the different experiments could not be excluded.

TABLE 12

*Summary of two-point data of Part II.*

| LOCI | TOTAL | PERCENT RECOM. |
|---|---|---|
| Aristaless-star | 4337 | 1.3 |
| Telegraph-star | 1169 | 0.9 |
| Expanded-star | 3060 | 1.5 |
| Dachsous-star | 4269 | 0.7 |

The next step was to build double recessive stocks of the recessive mutants. By use of such stocks, together with star, a series of three-point experiments could be made that would give decisive evidence as to the sequence of the three loci of each experiment and also relative distances found under the same condition with respect to crossover modifiers. In the process of building the double recessives, evidence could be obtained as to the relative order of certain of the genes.

### *Telegraph expanded double recessive*

The first double recessive sought was telegraph expanded. From the telegraph by star backcross of table 8 recombinational telegraph star flies were obtained which were mated to expanded. The $F_1$ star females were then crossed to telegraph males. If expanded were on the opposite side of star from telegraph

$$\frac{t_g \quad S \quad +}{+ \quad + \quad e_x},$$

as seemed probable from the preliminary results of BRIDGES, then the telegraph not-star flies which occurred in the offspring of this experiment as a result of crossing over between telegraph and star should have the constitution

$$\frac{t_g \quad e_x}{t_g \quad +}.$$

By breeding together such recombinational telegraph flies, the double recessive telegraph expanded should be obtained as about 25 percent of the telegraph offspring. But when this mating was made it was found that none of the offspring were expanded. This showed that the assumed order was incorrect, and that, in fact, the loci of telegraph and expanded are both on the same side of star. The loci of telegraph and expanded must

therefore be very close to each other, but there was no evidence as to which of the two is further from star. On the supposition that the order is expanded telegraph, an expanded star was crossed to telegraph, and the $F_1$ star female was backcrossed to expanded (table 13). The $F_2$ expanded flies were crossed to telegraph, but none gave telegraph offspring.

TABLE 13

*$P_1$, expanded star×telegraph; BC., $F_1$ star ♀×expanded ♂. (July 1925).*

| EXPANDED STAR | EXPANDED | EXPANDED STAR | EXPANDED | EXPANDED STAR | EXPANDED | EXPANDED STAR | EXPANDED |
|---|---|---|---|---|---|---|---|
| 99 | 1 | 43 | 1 | 63 | 2 | 73 | .. |
| 156 | .. | 89 | .. | 93 | 2 | 40 | 1 |
| 142 | 1 | 49 | .. | 79 | 1 | 70 | .. |
| 96 | .. | 62 | .. | 77 | 3 | 88 | 1 |
| 80 | 1 | 66 | 1 | 90 | .. | 93 | 1 |
| 35 | .. | 87 | .. | 79 | 1 | 56 | .. |
| 30 | 1 | 86 | 2 | 72 | .. | | |
| | | | | | | 2143 | 21 |

Similarly, on the supposition that the order is telegraph expanded, a telegraph star fly was crossed to expanded, and the $F_1$ star females were backcrossed to telegraph males (table 14). The $F_2$ telegraph not-star

TABLE 14

*$P_1$, telegraph star×expanded; BC., $F_1$ star ♀×telegraph ♂. (July 1925).*

| TELEGRAPH STAR | TELEGRAPH | TELEGRAPH STAR | TELEGRAPH | TELEGRAPH STAR | TELEGRAPH | TELEGRAPH STAR | TELEGRAPH |
|---|---|---|---|---|---|---|---|
| 82 | .. | 37 | .. | 74 | 1 | 59 | .. |
| 82 | 1 | 52 | 2 | 31 | .. | 87 | .. |
| 106 | .. | 34 | .. | 34 | .. | 35 | .. |
| 62 | 1 | 35 | .. | 35 | .. | 26 | .. |
| 38 | .. | 51 | 1 | 84 | 2 | 37 | .. |
| 14 | .. | 33 | 3 | 51 | .. | 62 | 1 |
| 37 | .. | 23 | .. | 82 | 4 | 49 | .. |
| 30 | 2 | 45 | .. | 67 | 4 | 39 | .. |
| 30 | .. | 90 | 3 | 77 | .. | | |
| | | | | | | 1810 | 25 |

flies that resulted from crossing over were crossed to expanded. In the off-spring of this cross ($F_3$) expanded flies were produced, which were inbred and which gave telegraph expanded in the next generation ($F_4$). The order is then established as telegraph, expanded, star (or star, expanded, telegraph). The stock of telegraph expanded was lost in traveling, and the three-point experiment could not therefore be carried out.

*Telegraph dachsous double recessive*

Telegraph flies were also crossed to dachsous, and the $F_1$ star females were backcrossed to telegraph males (table 15). The $F_2$ recombinational

TABLE 15

*$P_1$, telegraph star × dachsous; BC., $F_1$ star ♀ × telegraph ♂. (Mar. 1925).*

| TELEGRAPH STAR | TELEGRAPH | TELEGRAPH STAR | TELEGRAPH | TELEGRAPH STAR | TELEGRAPH |
|---|---|---|---|---|---|
| 74 | .. | 51 | 3 | 72 | 1 |
| 83 | .. | 56 | 1 | 65 | 1 |
| 65 | .. | 79 | 1 | | |
| | | | | 545 | 7 |

telegraph not-star flies were bred together, and in the next generation telegraph dachsous flies were obtained. This fact shows that dachsous is either on the opposite side from telegraph

$$\frac{t_g \quad + \quad d_s}{+ \quad S \quad +},$$

or, if telegraph and dachsous are on the same side of star, that dachsous is nearer to star than is telegraph

$$\frac{t_g \quad + \quad S}{+ \quad d_s \quad +}.$$

It had been supposed that the telegraph dachsous double recessive might be too difficult to distinguish from simple dachsous, since dachsous itself causes a slight erection of the scutellar bristles. However, it was found that often the bristles of the double form were extremely erected, even directed forward, and that telegraph could be identified in dachsous flies in about the same percentage (50±) as simple telegraph could be distinguished from wild type.

Telegraph star by dachsous backcross

The three-point backcross involving telegraph, dachsous and star (table 16) showed that telegraph and dachsous are on the same side of star, since the crossing over between them was much less frequent than between either and star. The telegraph dachsous recombination percentage was 0.1, while the telegraph star recombination percentage was 1.2 and the dachsous star 1.1. The telegraph star percentage was greater than the dachsous star percentage, which agrees with the order telegraph, dachsous, star. In a three-point backcross the class due to double crossing

TABLE 16

*$P_1$, telegraph star×dachsous; BC., $F_1$ star ♀×telegraph dachsous ♂. (April 1925).*

| TELEGRAPH STAR | TELEGRAPH DACHSOUS | TELEGRAPH | TELEGRAPH STAR | TELEGRAPH DACHSOUS | TELEGRAPH | TELEGRAPH STAR | TELEGRAPH DACHSOUS | TELEGRAPH |
|---|---|---|---|---|---|---|---|---|
| 75 | 1 | 2 | 92 | .. | 1 | 53 | .. | .. |
| 88 | .. | .. | 62 | .. | 2 | 73 | .. | 1 |
| 58 | .. | .. | 92 | .. | 1 | 88 | .. | 1 |
| 75 | .. | .. | 73 | .. | 2 | 64 | .. | 1 |
| 71 | 1 | 1 | 81 | .. | .. | 114 | .. | 1 |
| 69 | .. | 1 | 61 | .. | .. | | | |
| 58 | .. | 2 | 88 | .. | .. | 1435 | 2 | 16 |

over is the smallest class, and where the loci are very close together, as in the present case, it is not expected to be realized at all. The absence of flies of the telegraph dachsous star class shows that this was the double crossover class, and that the orientation of the genes was

$$\frac{t_g \quad + \quad S}{+ \quad d_s \quad +}.$$

*Aristaless dachsous double recessive*

A dachsous star fly (from table 10) was crossed to aristaless and the $F_1$ star females were crossed to dachsous. The dachsous not-star flies that occurred as the result of crossing over were inbred. None of their progeny were aristaless. From this it was evident that the locus of aristaless is not on the opposite side of star from dachsous

$$\frac{d_s \quad S \quad +}{+ \quad + \quad a_1}$$

but that it is on the same side. A second method consisted in crossing an aristaless star (from table 9) to dachsous and again mating the $F_1$ star females to aristaless males. The recombinational aristaless not-star flies were inbred, and in some cases there were produced the double recessive aristaless dachsous. The production of the double from the cross showed that the orientation of the genes was

$$\frac{a_1 \quad + \quad S}{+ \quad d_s \quad +}.$$

Aristaless star by dachsous backcross

The three-point backcross experiment (table 17) confirmed this order, since the double crossover classes, not realized, were aristaless dachsous star and wild type, and the orientation of the genes was accordingly

$$\frac{a_1 \quad + \quad S}{+ \quad d_s \quad +}.$$

TABLE 17

*$P_1$, aristaless star×dachsous; BC., $F_1$ star ♀×aristaless dachsous ♂. (April 1925).*

| ARISTALESS STAR | DACHSOUS | ARISTALESS DACHSOUS | STAR | ARISTALESS | DACHSOUS STAR | ARISTALESS STAR | DACHSOUS | ARISTALESS DACHSOUS | STAR | ARISTALESS | DACHSOUS STAR |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 130 | 153 | .. | 1 | 1 | 1 | 116 | 165 | .. | 1 | 2 | 2 |
| 106 | 170 | 1 | .. | .. | 2 | 159 | 204 | .. | 1 | 1 | 1 |
| 139 | 158 | .. | .. | 1 | 2 | 145 | 190 | 1 | 1 | 1 | 1 |
| 148 | 155 | 2 | .. | .. | 2 | 76 | 77 | .. | 3 | .. | 1 |
| 65 | 91 | .. | .. | .. | .. | 169 | 213 | .. | .. | 1 | 2 |
| 67 | 112 | .. | .. | 1 | 2 | 158 | 184 | .. | .. | 1 | 2 |
| 91 | 139 | 1 | .. | 1 | 1 | | | | | | |
| 137 | 149 | .. | .. | 2 | 3 | 1706 | 2160 | 5 | 7 | 12 | 22 |

The recombination percentages from table 14 were aristaless dachsous 0.3, aristaless star 1.2, and dachsous star 0.9 percent.

### *Aristaless expanded double recessive*

An expanded star fly, from table 11, was crossed to aristaless, and the $F_1$ star flies were backcrossed to expanded. The expanded not-star flies that occurred were then crossed to aristaless. None of the offspring of this later type of cross showed aristaless. From this result it was clear that aristaless and expanded lie on the same side of star; for if the orientation had been

$$\frac{e_x \quad S \quad +}{+ \quad + \quad a_1} \text{ or } \frac{a_1 \quad + \quad +}{+ \quad S \quad e_x}$$

then all the recombinational expanded flies would have produced aristaless.

The two-point data summarized in table 12, showed that the loci aristaless and expanded must be very close indeed to each other since the expanded star recombination percent was 1.5, and the aristaless star percent 1.3, which is very little different.

### Aristaless star by expanded backcross

A second experiment was started by mating a female that carried aristaless and star in one chromosome and expanded in the other to aristaless males. Twenty-nine of the recombinational aristaless not-star flies were mated to expanded, and at least two gave expanded flies. These were inbred, and in the next generation, aristaless expanded flies appeared. This fact showed that the orientation of the loci was

$$\frac{a_1 \quad + \quad S}{+ \quad e_x \quad +} \text{ or } \frac{S \quad + \quad a_1}{+ \quad e_x \quad +}.$$

Two three-point backcrosses (table 18) confirmed this order and gave an aristaless expanded recombination percent of 0.05, and an expanded star recombination percent of 1.7. The data in the second experiment (right column) gave unusually little expanded star crossing over, except in one culture (the last) that gave unusually much.

TABLE 18

*$P_1$, aristaless star×expanded; BC., $F_1$ star ♀×aristaless expanded ♂. (June 1925).*

| ARISTALESS STAR | EXPANDED | ARISTALESS EXPANDED | STAR | ARISTALESS EXPANDED | STAR | ARISTA-LESS STAR | EXPAN-DED | ARISTA-LESS EXPAN-DED | STAR | ARISTA-LESS | EXPAN-DED STAR |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 85 | 97 | .. | .. | 1 | 1 | 51 | 52 | .. | 1 | .. | 1 |
| 25 | 31 | .. | .. | .. | 1 | 28 | 25 | .. | .. | 1 | 1 |
| 61 | 62 | .. | .. | .. | 3 | 87 | 70 | .. | .. | 1 | .. |
| 106 | 86 | .. | .. | 1 | 2 | 109 | 96 | .. | .. | .. | .. |
| 13 | 17 | .. | .. | .. | .. | 18 | 10 | .. | .. | .. | .. |
| 116 | 89 | .. | .. | 4 | 1 | 46 | 37 | .. | .. | .. | .. |
| 87 | 57 | .. | .. | 2 | 3 | 50 | 76 | .. | .. | .. | .. |
| 27 | 26 | .. | .. | 1 | 2 | 104 | 114 | .. | .. | 7 | 3 |
| 17 | 16 | .. | .. | 1 | .. | | | | | | |
| 75 | 71 | .. | .. | .. | .. | 1105 | 1032 | .. | 1 | 19 | 18 |

### *Expanded dachsous double recessive*

The previous experiments had shown that aristaless and dachsous lie on the same side of star; likewise that aristaless and expanded lie on the same side of star. From this it follows that expanded and dachsous are on the same side of star.

The data of table 12 had given 1.5 percent of recombination for expanded star and 0.7 for dachsous star. Accordingly the attempt to obtain an expanded dachsous stock was made on the assumption that the locus of expanded is further from star than is the locus of dachsous. Expanded star flies were bred to dachsous and the $F_1$ star females were backcrossed to expanded males. The expanded not-star flies produced as the result of crossing over were inbred (4 ♀×4 ♂). It was expected that part of the expanded flies should be of the constitution

$$\frac{e_x \quad d_s}{e_x \quad +},$$

coming from crossing over between the loci of two recessives in the

$$\frac{e_x \quad + \quad S}{+ \quad d_s \quad +}$$

mother. The remainder should be of the constitution

$$\frac{e_x \quad +}{e_x \quad +}$$

coming from crossing over between the loci of dachsous and star. If two of the first type be bred together, then the double recessive would be produced in the next generation. The inbreeding did not produce the double type. Evidently if there were present flies of the first type they had mated only with flies of the second type. The flies were then remated to dachsous, and in the offspring of some, dachsous flies appeared

$$\frac{e_x \quad d_s}{+ \quad d_s}$$

These were inbred and the double recessive was obtained. This fact showed that the order is, as assumed, expanded, dachsous, star (or star, dachsous, expanded).

It had been anticipated that there would be considerable difficulty in distinguishing the double recessive expanded dachsous from expanded, since the main characteristic of dachsous is crossveins close together, and this feature is likewise present in expanded. However, it was found that the shortness of wings in dachsous was very apparent in the double form, which had wings practically as broad as long. The expanded dachsous flies were small and rather low in viability and inclined to sterility, so that much trouble was experienced in carrying on stocks and securing crosses. This difficulty was solved by crossing expanded dachsous to curly, a second-chromosome dominant character that is lethal when homozygous and whose gene occurs in a chromosome that also carries crossover suppressors. The $F_1$ curly flies, when bred together, gave a stock that was mostly curly flies heterozygous for expanded dachsous with a few expanded dachsous homozygotes.

*Expanded star by dachsous backcross*

For determining the recombination percentages for expanded dachsous and star, an

$$\frac{e_x \quad + \quad S}{+ \quad d_s \quad +}$$

backcross was carried out (table 19). The males used in backcrossing were usually curly over expanded dachsous, and the curly offspring were discarded before making the separations for the three other characters. The data gave 0.2 as the expanded dachsous, and 1.2 as the dachsous star recombination percent.

TABLE 19

*$P_1$, expanded star×dachsous; BC., $F_1$ star ♀ ×expanded dachsous curly. (July 1925).*

| EXPANDED STAR | DACHSOUS | EXPANDED DACHSOUS | STAR | EXPANDED | DACHSOUS STAR | EXPANDED STAR | DACHSOUS | EXPANDED DACHSOUS | STAR | EXPANDED | DACHSOUS STAR |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 121 | 129 | 1 | .. | 3 | 3 | 17 | 28 | .. | .. | 1 | .. |
| 57 | 61 | .. | .. | .. | 1 | 48 | 51 | .. | .. | 1 | .. |
| 58 | 80 | .. | .. | 2 | .. | 53 | 64 | .. | .. | .. | .. |
| 42 | 64 | .. | .. | .. | .. | 49 | 54 | 1 | .. | .. | 1 |
| 52 | 61 | .. | 1 | .. | .. | 56 | 45 | .. | .. | .. | 2 |
| 44 | 57 | .. | .. | 1 | 1 | 61 | 64 | .. | .. | 4 | 1 |
| 60 | 71 | .. | 1 | .. | 2 | 62 | 68 | .. | .. | 1 | .. |
| 30 | 44 | .. | .. | .. | .. | 51 | 64 | .. | .. | 1 | .. |
| 65 | 89 | .. | 1 | 1 | .. | 55 | 70 | .. | .. | .. | .. |
| 46 | 57 | .. | 1 | .. | .. | 43 | 66 | .. | .. | .. | 2 |
| 48 | 67 | .. | .. | 1 | .. | | | | | | |
| | | | | | | 1118 | 1354 | 2 | 4 | 16 | 13 |

## THE ORDER OF THE LOCI

The three-point experiments reported in Part II allowed the order of the loci telegraph, aristaless, expanded, dachsous and star to be deduced. Dachsous was found to lie on the same side of star as telegraph

$$\frac{t_g \quad + \quad S}{+ \quad d_s \quad +},$$

table 16, as aristaless

$$\frac{a_1 \quad + \quad S}{+ \quad d_s \quad +}$$

table 17, and as expanded

$$\frac{e_x \quad + \quad S}{+ \quad d_s \quad +}$$

table 19. Furthermore, in each case it was found to lie nearer to star than does each of these other loci. Similarly, expanded lies on the same side of star as does telegraph

$$\frac{t_g \quad + \quad S}{+ \quad e_x \quad +}$$

table 14 and aristaless

$$\frac{a_1 \quad + \quad S}{+ \quad e_x \quad +},$$

table 18 and is nearer than is either telegraph or aristaless.

### *Aristaless dumpy by star backcross*

The final point to be determined was whether the group of the loci aristaless, telegraph, expanded and dachsous lies to the left or to the right of star. Star had been regarded as the zero point, and the other genes of the second chromosome arranged in order to the "right" of it. By using in a three-point backcross with star any member of the group in question and any locus known to be to the right of star, the relative order could be determined. Accordingly, an aristaless dumpy by star backcross was carried out (table 20). None of the more than 2000 flies of this backcross

TABLE 20

*$P_1$, star×aristaless dumpy; BC., $F_1$, star ♀×aristaless dumpy ♂. (Nov. 1925).*

| ARISTALESS DUMPY | STAR | ARISTALESS STAR | DUMPY | ARISTALESS | STAR DUMPY |
|---|---|---|---|---|---|
| 83 | 105 | 2 | 2 | 17 | 16 |
| 96 | 93 | .. | .. | 19 | 7 |
| 111 | 131 | .. | 1 | 14 | 12 |
| 113 | 101 | .. | .. | 22 | 16 |
| 101 | 137 | 2 | 2 | 16 | 16 |
| 147 | 164 | 1 | .. | 20 | 9 |
| 120 | 107 | 1 | .. | 12 | 11 |
| 147 | 118 | 1 | .. | 12 | 13 |
| 918 | 956 | 7 | 5 | 132 | 100 |

showed all three characters or were wild type. Therefore these classes constitute the double crossover classes, and the order of loci is

$$\frac{a_1 \quad + \quad d_p}{+ \quad S \quad +}.$$

Thus, star is no longer the zero point of the second chromosome. On the basis of the data of this paper a new map may now be constructed.

### CONSTRUCTION OF MAP

In table 21, the recombination data of the preceding sections have been summarized.

In determining the distances between loci two lots of data have been disregarded, namely, all recombination percentages in which the untrustworthy character telegraph is involved, (telegraph dachsous and telegraph star), and the expanded star data of table 7, that had been collected before sufficient familiarity with expanded and its interactions with star had been acquired.

TABLE 21

*Summary of recombination data**.

| LOCI | EXPERIMENT | TABLE NO. | TOTAL | RECOMBINATIONS | PERCENT RECOMBINATION |
|---|---|---|---|---|---|
| Telegraph dachsous | [tel. star/dach. | 16 | 1453 | 2 | 0.1] |
| Telegraph star | [tel./star | 1 | 274 | 3 | 1.1] |
| | [tel./star | 2 | 941 | 5 | 0.5] |
| | [tel./star | 8 | 1169 | 11 | 1.0] |
| | [tel. star/exp. | 14 | 1835 | 25 | 1.4] |
| | [tel. star/dach. | 15 | 552 | 7 | 1.3] |
| | [(tel. star/dach. | 16 | 1453 | 18 | 1.2)] |
| Aristaless expanded | aris. star/exp. | 18 | 2175 | 1 | 0.05 |
| Aristaless dachsous | aris.star/dach. | 17 | 3912 | 12 | 0.3 |
| Aristaless star | aris./star | 3 | 334 | 3 | 0.9 |
| | aris./star | 9 | 4337 | 58 | 1.3 |
| | aris.dumpy/star | 20 | 2118 | 12 | 0.6 |
| | Total | | 6789 | 73 | 1.1 |
| | (aris.star/exp. | 18 | 2175 | 37 | 1.7) |
| | (aris.star/dach. | 17 | 3912 | 46 | 1.2) |
| | (Total | | 6087 | 83 | 1.4) |
| | Grand total | | 12876 | 156 | 1.2 |
| Expanded dachsous | exp. star/dach. | 19 | 2507 | 6 | 0.2 |
| Expanded star | [exp./star | 7 | 1346 | 54 | 4.0] |
| | exp./star | 11 | 3060 | 46 | 1.5 |
| | tel./exp. star | 13 | 2164 | 21 | 1.0 |
| | Total | | 5224 | 67 | 1.3 |
| | (exp.star/dach. | 19 | 2507 | 35 | 1.4) |
| | Grand total | | 7731 | 102 | 1.3 |
| Dachsous star | dach./star | 10 | 4269 | 31 | 0.7 |
| | tel. star./dach. | 16 | 1453 | 16 | 1.1 |
| | aris. star/dach. | 17 | 3912 | 34 | 0.9 |
| | exp. star/dach. | 19 | 2507 | 29 | 1.2 |
| | dach.$^3$/star | 6 | 396 | 3 | 0.8 |
| | Total | | 12537 | 113 | 0.9 |
| Star dumpy | aris.dumpy/star | 20 | 2118 | 232 | 11.0 |

*The data enclosed by square brackets [] are considered untrustworthy. The data enclosed by parentheses () are "secondary" and are not used in calculating distances.

There is no certain evidence as to the relative order of aristaless and telegraph. But since aristaless is a trustworthy character that will be used extensively, and telegraph is relatively very poor, aristaless has been chosen as the zero of the new map. The locus of telegraph is probably of the order of 0.1 unit distant, and has been arbitrarily put to the right at 0.0±.

The aristaless expanded recombination percent was 0.05, based on 2715 flies. Since at least two flies in the 29 tested in securing the aristaless expanded double recessive, proved to be crossovers between aristaless expanded, an independent calculation of the aristaless expanded distance can be made (2 : 29 :: x : 1.3; x = 0.09). In view of the high probable errors of such small percentages, an accuracy to 0.1 unit is beyond reach, so the nearest tenth, namely, 0.1, has been taken as the locus of expanded.

The next locus to the right is dachsous, which is 0.3 to the right of aristaless (3912 flies) and 0.2 to the right of expanded (2507 flies). These two determinations agree at the value +0.3 as the locus of dachsous.

The dachsous star data (12,537 flies) place star at 0.9 to the right of dachsous, or at 1.2 (0.3+0.9). The expanded star data (5,224) place it at 1.3 to the right of expanded, or at 1.4 (0.1+1.3). The aristaless star data (6,789) place star at 1.2 (0.0+1.2). The weighted average of these data places the locus of star at +1.3 (to the nearest tenth).

The final map is given in figure 1.

## SUMMARY AND EVALUATION OF THE MUTANTS

The serial order and relative distances have been established for a group of five mutant loci, namely, star, telegraph, aristaless (aristaless[2]), dachsous (dachsous[2], dachsous[3]) and expanded. These linkage relations are expressed in the map given in figure 1, in which aristaless is the new zero point of the second chromosome and the locus of star is at 1.3.

The most useful of these mutants is star, primarily because of its dominance, which enables the mutant to be followed through extended and complex experiments with a minimum of labor in preparing stocks.

The next most useful mutant is aristaless, primarily because its locus is the one furthest to the left in the map. A second advantage is that it can be used more successfully than star with plexus, which is a very important mutant and which is partly suppressed by star. A disadvantage of aristaless is that its viability is poorer than that of star, being roughly 90 percent that of the wild type. In speed of classification aristaless is very high, in which respect star is fairly poor.

Dachsous had the best viability (99 percent) of any of the mutants at

the left end, and dachsous[2] is probably slightly better even than dachsous. The classification of each is certain and fairly rapid. The disadvantage of the dachsous mutants is that dumpy, which is the most important mutant between star and black, also has crossveins that are close together, and it is probable, though not definitely known, that dachsous would be unworkable with dumpy. Dachsous[3] has very poor viability (50 percent) and hence will not be used except in situations in which its female-sterility is an advantage.

Expanded offers no advantages over aristaless or dachsous, though its viability is high (97 percent) and its general characteristics good.

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# SOME NUMERICAL RESULTS OF SELECTION UPON POLYHYBRIDS[1]

CONWAY ZIRKLE
*Harvard University, Bussey Institution, Forest Hills, Massachusetts*

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TABLE OF CONTENTS

| | PAGE |
|---|---|
| INTRODUCTION | 531 |
| PART I | |
| The elimination in each generation of all individuals dominant for all of the $m$ independent factors dealt with in a polyhybrid of $m$ allelomorphs | 534 |
| 1. The dihybrid | 534 |
| 2. The trihybrid | 539 |
| 3. The tetrahybrid | 541 |
| 4. Polyhybrids for any number $m$ pairs of allelomorphs | 542 |
| PART II | |
| The elimination in each generation of all individuals who are not dominant for all of the $m$ independent factors in a polyhybrid of $m$ allelomorphs | 557 |
| 1. The dihybrid | 558 |
| 2. The trihybrid | 559 |
| 3. The tetrahybrid | 560 |
| 4. The polyhybrid | 561 |
| PART III | |
| The elimination in each generation of all individuals recessive for all $m$ independent factors in a polyhybrid of $m$ allelomorphs | 563 |
| 1. Method of deriving zygotes of generation $F_n$ from gametes of generation $G_n$ | 563 |
| 2. Method of deriving gametes of generation $n+1$ from gametes of generation $G_n$ | 564 |
| PART IV | |
| The elimination in each generation of all individuals (A) containing two or more independent dominant factors, and (B) containing three or more independent dominant factors in a polyhybrid of $m$ allelomorphs | 567 |
| GENERAL SUMMARY | 572 |
| 1. Summary of formulæ | 577 |
| LITERATURE CITED | 583 |

## INTRODUCTION

It is a well known fact that those portions of the human population that have distinguished themselves in intellectual pursuits reproduce much less freely than do the remainder of the population. The question arises: What effect has this on the population as a whole? It is generally assumed that this adverse selection lowers the general level of intellectual

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power, so that a steady deterioration in that respect is in progress. Is this correct, and if so, at what rate does the deterioration occur? Or is it possible, as some have suggested, that intellectual power is due to the unusual combinations of genes which continually arise in the general population, and that the frequency of these combinations is little affected by the fact that the individuals resulting from them do not propagate freely? How much is it affected?

How can this problem be attacked? In man the common individual differences are generally multiple factor cases whose elements are unknown to us (MORGAN 1924). Intellectual power is doubtless due to special combinations of numerous factors; the problem is: If those special combinations do not propagate freely, what effect has this on the frequency of occurrence of such combinations? To obtain the general principles here at work, the problem must first be made definite and simplified; basing on the results thus obtained, the more complex problems may be attacked. We may first examine the effect produced when a particular combination of several factors is completely excluded from further propagation. For example, what is the effect on the occurrence of a characteristic that is due to the simultaneous presence of $m$ dominant factors, if the individuals which have all these factors do not breed further? Or what is the effect if a given characteristic is due to the simultaneous occurrence of $m$ particular dominant factors and $n$ particular recessive ones, and the individuals with this combination do not further breed? Or suppose that some definite proportion—say one-half—of them breed while the rest do not?

As perhaps the simplest case, let us take that in which the characteristic in question depends upon the occurrence together of a certain number of dominant factors. An instance of this sort is found in the agouti color of rats, guinea pigs, and rabbits (CASTLE and WRIGHT 1916). What is the effect upon a population, heterozygous as to $m$ independent factors which determine the agouti color, when, in the $F_2$ and all subsequent generations, no agouti individuals are allowed to breed, and the rest of the population breed at random? An answer to the above question, even if generalized to fit any number of factors, would by no means solve our original problem. In the human stock the problem may be complicated by such factors as (1) linkage, (2) selective mating, (3) the fact that the superior individuals (in question) do not fail to reproduce entirely but only reproduce at a slower rate, and (4) the possibility that some of the factors involved are recessive, others dominant. However, the solution of the problem of the effect upon a polyhybrid stock of eliminating in every generation all

individuals who are dominant for all factors concerned will perhaps form a basis upon which the more complex problems may be attacked.

The greater part of the work done to date upon the effects of various schemes of selection has been upon monohybrid stocks. PEARSON (1904) showed that the several types in a Mendelian population in which the $F_2$ generation was composed of 25 percent *aa*, maintains a constant proportion under conditions of random mating and no selection. JENNINGS (1916) derived a number of formulæ showing the results of various systems of breeding in monohybrids. WARREN (1917) showed that the elimination of a homozygous type in a monohybrid under conditions approximating those of natural selection, caused a progressive decrease in the number of such individuals appearing. HALDANE (1924) found mathematical expressions for the effect of selection on simple Mendelian populations mated at random. JENNINGS (1917) showed the effect of diverse systems of breeding, with respect to two pairs of characters. WRIGHT (1921) demonstrated that, in a polyhybrid stock, when dominance was lacking, the two extreme types were the only ones which could be permanently fixed.

In the present paper formulæ are derived for obtaining the results of the following systems of selection.

I. *The elimination in each generation of all individuals dominant for all of the m independent factors dealt with in a polyhybrid of m allelomorphs.* The value of *m* in this case must be less than 5. While it is relatively an easy matter to derive formulæ for higher hybrids the formulæ soon become too cumbersome, since they are for deriving any generation in terms of the preceding generation.

II. *The elimination in each generation of all individuals who are not dominant for all of the m independent factors in a polyhybrid of m allelomorphs.* These formulæ are in terms of *n*, the number of the filial generation: that is, in order to obtain the proportion of the types appearing in any generation it is not necessary to know the percentage in any other generation.

III. *The elimination in each generation of all individuals recessive for all m independent factors in a polyhybrid of m allelomorphs.* These formulæ are also in terms of *n*, where *n* is equal to *2* and *3*; when *n* is larger each generation will have to be derived in terms of the preceding generation.

IV. *The elimination in each generation of all individuals (A) containing two or more independent dominant factors, and (B) containing three or more independent dominant factors in a polyhybrid of m allelomorphs.* The formulæ are for deriving any generation in terms of the preceding generation.

Tables showing the percentages of the given types appearing in each generation are given.

## PART I.

### THE ELIMINATION IN EACH GENERATION OF ALL INDIVIDUALS DOMINANT FOR ALL OF THE *m* INDEPENDENT FACTORS DEALT WITH IN A POLYHYBRID OF *m* ALLELOMORPHS

*How rapidly will the completely dominant individuals disappear from the population if none of such dominants produced leave progeny?*

In dealing with this problem, we shall first deal with cases involving but few pairs of factors, then with more complex cases. By comparison of the results for successively larger number of factors, we shall develop a method applicable to polyhybrids with any number (*m*) of allelomorphs. In transforming one generation into the next, we shall use throughout the general method introduced by JENNINGS (1917), of dealing primarily with the gametes, the zygotes of any given generation being readily obtainable from the knowledge of the gametes that produce them. This method reduces enormously the complexity of the problems, as compared with working primarily with the zygotes. In the present paper, however, this method is further greatly simplified in such a way as to make it a practicable one for dealing with polyhybrids of many pairs of allelomorphs.

#### Designation of the zygotic and gametic generations

We begin in each case with a completely heterozygotic parent, as *Aa Bb*, produced by crossing *ABAB* with *abab*. This original heterozygote we shall call the $F_1$ generation. The gametes produced by the $F_1$ generation of zygotes we shall call the $G_1$ gametes; these produce by their mating the $F_2$ zygotes, these the $G_2$ gametes, and so on. The order of alternate zygotic and gametic generations is thus:

$$F_1 \rightarrow G_1 \rightarrow F_2 \rightarrow G_2 \rightarrow F_3 \rightarrow G_3, \text{ and so on.}$$

#### 1. *The dihybrid*

In the progeny of the monohybrid, *Aa*, of course one elimination of the dominant zygotes gets rid completely of the dominant factor *A*, leaving only recessives. For the dihybrid *AaBb*, the problem of determining the constitution of each generation in terms of that preceding it, in case all the individuals (zygotes) dominant for both *A* and *B* are eliminated in each generation, may be attacked by the method of JENNINGS (1917).

The original parents are *AABB* and *aabb*, yielding by their cross the $F_1$ generation *AaBb*. These $F_1$ individuals produce in equal numbers the

four sorts of $G_1$ gametes: $AB$, $Ab$, $aB$, and $ab$. Call the respective proportions of these $P$, $Q$, $R$, and $S$, then the proportions of the different kinds of zygotes yielded by the random mating of these four sorts of gametes (as shown in the usual dihybrid table of zygotes) are given by the various terms of the expansion of $(P+Q+R+S)^2$. They are the following:

TABLE 1

*Dihybrid.*

| ZYGOTES OF $F_2$ | IN TERMS OF GAMETE $G_1$ (PRODUCED BY $F_1$) |
|---|---|
| $a$ $(=AABB)$ | $= P^2$ |
| $b$ $(=2AABb)$ | $= 2PQ$ |
| $c$ $(=AAbb)$ | $= Q^2$ |
| $d$ $(=2AaBB)$ | $= 2PR$ |
| $e$ $(=4AaBb)$ | $= 2PS+2QR$ |
| $f$ $(=2Aabb)$ | $= 2QS$ |
| $g$ $(=aaBB)$ | $= R^2$ |
| $h$ $(=2aaBb)$ | $= 2RS$ |
| $i$ $(=aabb)$ | $= S^2$ |

Designate the proportions of each of these nine kinds of zygotes respectively by the letters $a$ to $i$, as shown in table 1; these proportions, in terms of the proportions of the gametes from which they are formed, are given at the right. Now from these zygotes we eliminate all double dominants—those containing $AB$; that is, we eliminate the zygotes designated $a$, $b$, $d$, and $e$, leaving only $c$, $f$, $g$, $h$, and $i$. If each of these produces two gametes, the natural proportions will be retained; we shall then find that the proportions $P$, $Q$, $R$, and $S$ of the four sorts of gametes produced are those given in the second column of table 2.

TABLE 2

| (1) GAMETES OF $G_2$ (FROM $F_2$) | (2) IN TERMS OF PROPORTIONS OF ZYGOTES OF $F_2$ | (3) IN TERMS OF PROPORTIONS OF GAMETES OF $G_1$ (FROM $F_1$) |
|---|---|---|
| $P$ $(=AB)$ | 0 | 0 |
| $Q$ $(=Ab)$ | $2c+f$ | $2Q^2+2QS$ |
| $R$ $(=aB)$ | $2g+h$ | $2R^2+2RS$ |
| $S$ $(=ab)$ | $f+h+2i$ | $2QS+2RS+2S^2$ |

We have now but to transform the proportions of the zygotes of $F_2$, given in the second column into those of the gametes of $G_1$ (as shown in table 1), in order to have the proportions of the gametes of $G_2$ stated in terms of the proportions of the gametes of $G_1$; these are given in the third column of table 2. Since it is only the relative proportions that we

require, the factor 2 may be taken out, yielding table 3 as our basic table by which, from the proportions of the gametes of one generation, the proportions of those of the next generation may be derived.

TABLE 3

*Dihybrid. Proportions of the gametes of generation n+1, in terms of those of generation n, in case all zygotes having both factors dominant have been eliminated.*

| GAMETES OF GENERATION $n+1$ | IN TERMS OF THOSE OF GENERATION $n$ |
|---|---|
| $P_{n+1}$ | 0 |
| $Q_{n+1}$ | $Q_n\ (Q_n+S_n)$ |
| $R_{n+1}$ | $R_n\ (R_n+S_n)$ |
| $S_{n+1}$ | $S_n\ (Q_n+R_n+S_n)$ |

When we start with the $F_1$ dihybrid $AaBb$, the four sorts of gametes of $G_1$, produced by it, are numerically equal; application of table 3 therefore yields the following proportions for successive generations:

TABLE 4

*Dihybrid.*

| | GAMETES OF | | | |
|---|---|---|---|---|
| $G_1$ | $G_2$ | $G_3$ | $G_4$ | $G_5$ |
| $P = 1$ | 0 | 0 | 0 | 0 |
| $Q = 1$ | 2 | 10 | 310 | 368,510 |
| $R = 1$ | 2 | 10 | 310 | 368,510 |
| $S = 1$ | 3 | 21 | 861 | 1,281,641 |

At any generation desired, the proportion of the different sorts of zygotes is obtained by the use of table 1. What we desire to know is the proportion in each generation of the zygotes that contain the double dominant $AB$, and are hence to be eliminated. In the $F_2$ generation, all zygotes into which the gamete $P(=AB)$ enter are eliminated, and no such gametes or zygotes again appear. In these later generations, the total proportions of the different sorts of zygotes are therefore given by the several terms of the expansion of $(Q+R+S)^2$. The double dominants are now formed only as the combination $e(=AaBb)$ of table 1, and in the proportion $2QR$ (since the combination $2PS$ of table 1 no longer appears). The proportions of the double dominants and of the other combinations for any zygotic generation are therefore obtained from the proportions of the gametes yielded by the previous generation, by table 5.

TABLE 5

*Dihybrid.*

| ZYGOTES OF GENERATION $n+1$ | IN TERMS OF GAMETES FROM GENERATION $n$ | EXAMPLE: ZYGOTES IN GENERATION $F_4$ | |
|---|---|---|---|
| | | TOTAL | PERCENT |
| Containing $AB$ | $2QR$ | 200 | 11.9 |
| Not containing $AB$ | $Q^2+R^2+S^2+2QS+2RS$ | 1481 | 88.1 |
| Total | $(Q+R+S)^2$ | 1681 | 100 |

As an example, the zygotic proportions in $F_4$ (as derived from table 4) are given at the right.

*Simplification of the method, by the use of common designations for all gametes containing the same number of dominant factors:* The above method can be greatly simplified (as seen particularly in work with numerous allelomorphs) by the following consideration.

1. All different kinds of gametes having the same number of dominant (and therefore of recessive) factors such as *Ab* and *aB*, are similarly affected by any form of selection that eliminates all zygotes showing a certain specified number of dominant factors, *irrespective of which particular factors there are.*

2. Therefore, if at the beginning these diverse kinds of gametes are present in equal proportions, their proportions remain equal throughout the entire selective breeding. This is actually the case when we begin, as in the present work, with a parent that is heterozygotic for all its factors.

3. Such equal groups of gametes can be given the same designation, and the proportion of each can then be determined by the one operation of determining the proportion corresponding to this designation. Thus the number of diverse unknown quantities with which we must work is greatly reduced. The total number of different kinds of gametes produced by a zygote that is heterozygotic for $m$ factors is $2^m$: by the procedure just mentioned this reduced to but $m+1$ different classes. For our purposes one kind of gamete—that in which all the factors are dominant—does not appear at all; the reduction is therefore from $2^m-1$ kinds to $m$ classes. While in the dihybrid the reduction is thus only from 3 unknown quantities to 2, in the octahybrid the reduction is from 255 to 8, bringing the treatment of these and still more complex cases within the bounds of practicability.

In accordance with these principles, therefore, in the dihybrid the proportion of each of the two gametes *Ab* and *aB* (which we have called *Q* and *R*) can be given a single designation (*q*). In the tetrahybrid the proportions of the four gametes *ABCd*, *ABcD*, *AbCD*, and *aBCD* will likewise be given a common designation (*q*).

*Designation of gametes:* For further development of the matter, it is desirable to have some uniform system of designating the proportions of the different classes of gametes. Suppose that we begin with a parent that is a polyhybrid, *AaBbCc*, etc., for $m$ pairs of factors. Then the diverse gametes will contain respectively $m$, $m-1$, $m-2$ . . . . , to 0

dominant factors. We shall employ for these respectively the designations given below: (table 6)

TABLE 6
*Designation of Gametes.*

| | | | | | | |
|---|---|---|---|---|---|---|
| No. of dominant factors..... | $m$ | $m-1$ | $m-2$ | $m-3$ | $m-4$ | and so on |
| Designation of gamete..... | $p$ | $q$ | $r$ | $s$ | $t$ | and so on |

Thus in a dihybrid $AB=p$, $Ab$ and $aB$ each $=q$, $ab=r$; in a tetrahybrid $ABcd=r$; in a hexahybrid, $aBCdeF=s$, and so on.

Since in the dihybrid, as just set forth, the proportions of each of the two gametes that are designated $Q$ and $R$ in table 2 are now to be designated $q$, while the one there designated $S$ is to be called $r$, table 3 assumes the abridged form given in table 7.

TABLE 7
*Dihybrid.*

| GAMETES OF GENERATION $n+1$ | IN TERMS OF GAMETES OF GENERATION $n$ |
|---|---|
| $p$ | 0 |
| $q$ | $q(q+r)$ |
| $r$ | $r(2q+r)$ |

(where $q$=proportion of $Ab$ or of $aB$; $r$=proportion of $ab$)

By making the same substitution in table 5, we find that the proportion of double dominant zygotes ($AB$) present (and to be eliminated) in any generation is (in terms of the gametes which produce that generation):

$$\frac{2q^2}{(2q+r)^2} \tag{8}$$

Formula 8 makes it possible to determine with some labor for a series of successive generations the proportion of completely dominant individuals remaining, and the curve of their rate of disappearance.

A formula for obtaining at once the gametic proportions in any generation $G_n$ (and thence the zygotic proportions), without determining it for the intervening generations, would be extremely useful. An approximate formula of this sort may be derived in the following way, for which I am indebted to Doctor F. D. MURNAGHAN of the Mathematics Department of the JOHNS HOPKINS UNIVERSITY. In table 7, at the right, let $r/q$ for generation $n$ be represented by $l_n$: then on dividing the first equation by the second, we obtain

$$l_{n+1}=\frac{l_n(2+l_n)}{1+l_n}=1+l_n-\frac{1}{1+l_n} \tag{9}$$

Substituting the values of $q$ and $r$, the same proportions are yielded for the successive generations as are given in table 4.

In formula 9, when $n$ becomes large, it is found that the value of $l_n$ approaches $n-1$. Now our ratio

$$\frac{2q^2}{(2q+r)^2}$$

of formula 8, if expressed in terms of $l_n$, becomes

$$\frac{2}{(2+l_n)^2}$$

Substituting, in this expression, for $l_n$ the value $n-1$ we obtain for the dihybrid as the proportion of double dominants in any generation $n$ (when $n$ is large) the following:

$$\frac{2}{(1+n)^2} \tag{10}$$

Where $n$ is small this equation of course cannot be used.[1] Experience shows that if we place in the denominator the quantity $-\sqrt{n/2}$, yielding the formula

$$\frac{2}{\left(n-\sqrt{\frac{n}{2}}+1\right)^2} \tag{11}$$

the results come throughout, when $n>7$, extremely close to the correct values obtained by the repeated use of table 7, and formula 8. (See table 35.)

### 2. *The trihybrid*

The problem of the results of eliminating in each generation all the completely dominant individuals (those containing $ABC$) in the trihybrid, is attacked by the same methods employed for the dihybrid. We begin with the $F_1$ triple heterozygote $AaBbCc$. This produces in equal numbers 8 sorts of gametes of $G_1$ that are represented in table 12. We may designate these eight kinds provisionally by the first eight letters of the alphabet,

[1] The problem of deriving the gametic proportion in any generation ($G_n$) from the formulæ

$$q_{n+1}=q_n(q_n+r_n)$$
$$r_{n+1}=r_n(2q_n+r_n)$$

without determining it for all previous generations was proposed by MURNAGHAN (1923) in THE AMERICAN MATHEMATICAL MONTHLY. An approximate solution in terms of $n$ has been given by BENNETT (1924).

*a* to *h* (these designations are later to be discarded). These eight fall into 4 groups, containing respectively 3,2,1, and 0 dominant factors, as shown in the table. In accordance with the principles set forth on an earlier page, the proportions of any one kind of gamete of each of these groups may be given a common designation: in accordance with table 6, the groups will be *p*, *q*, *r*, and *s*, as shown in the lower row of table 12.

TABLE 12

*Gametes ($G_1$) from the trihybrid AaBbCc with their designations and classifications into groups.*

| | | | | |
|---|---|---|---|---|
| 1. No. of dominant factors | 3 | 2 | 1 | 0 |
| 2. Designations and consitution of different kinds | *a. ABC* | *b. ABc*<br>*c. AbC*<br>*d. aBC* | *e. Abc*<br>*f. aBc*<br>*g. abC* | *h. abc* |
| 3. Number of kinds of gametes in each group | 1 | 3 | 3 | 1 |
| 4. Designation of the gametes according to groups | *p* | *q* | *r* | *s* |

The random mating of these 8 gametes produces in the $F_2$ generation 64 zygotes, of which 27 contain *ABC* and are therefore eliminated.

To obtain the proportions of complete dominants in the later generations, we may proceed on the following considerations. In $F_2$, all the zygotes into which the gamete $p(=ABC)$ enters are eliminated, and in later generations that gamete does not again enter into the formation of zygotes. We may therefore omit this gamete from consideration, determining only the proportion of complete dominants (to be eliminated) that result from the mating of the other three groups. In producing the $F_2$ generation, these three groups taken by themselves produce precisely the zygotes which are not eliminated by the process of removing all those into which enters the gamete $p(=ABC)$. We may represent these three groups thus: $3q+3r+s$. The total number of zygotes of $F_n$ which their mating produces s then $(3q+3r+s)^2$.

If we designate each of these gametes separately by the provisional designations given at 2, of table 12, they yield in mating zygotes whose proportions are given by the expansion of $(b+c+d+e+f+g+h)^2$. Detailed study will show that the following contain the three dominants *ABC*

$$2bc,\ 2bd,\ 2bg,\ 2cd\ 2cf,\ 2de$$

Replacing these letters by their group equivalents (lower row of table 12), we obtain for the zygotes containing dominants (and hence to be eliminated):

$$6q^2+6qr;\ \text{or}\ 6q(q+r) \tag{13}$$

In the gametes from the $F_1$ heterozygote, *AaBbCc*, the value of each of the designations *q*, *r*, and *s* is 1. In later generations these values will

be different, but the expression (13) remains correct when the proper values are substituted for $q$, $r$, and $s$. Thus in any generation the proportion of zygotes eliminated, in terms of the gametes from whose mating they are derived, is:

$$\frac{6q(q+r)}{(3q+3r+s)^2} \tag{14}$$

In order to simplify the problem of expressing the gametes of any generation in terms of those of the preceding generation it is necessary that we ignore for the time being certain very important factors, which will later be evaluated. The gametes will first be treated as if they were immutable units, that is, that the gametes which fuse to form a zygote appear unchanged in the next generation—that a zygote can produce only the gametes out of which it itself was formed—as if linkage between all factors were complete. This assumption is of course true when the zygote is either homozygous or heterozygous for a single pair of factors. When, however, the zygote is heterozygous for two or more factors certain rearrangements of genes occur so that some of the gametes produced in the next generation are different from those which formed the zygote in question. For example, in the trihybrid the gametes *aBc* and *abC* are represented by $r$. The zygote *aaBbCc* formed from them would be represented by $r^2$. This zygote could produce gametes $q(aBC)$ and $s(abc)$ as well as $r(aBc)$ and $(abC)$. This "shifting" of factors will be treated later.

Now, by methods parallel to those employed for obtaining tables 3 and 7 in the dihybrid, we obtain, for the trihybrid, table 15 for transforming the gametic proportions of one generation into those of the next.

TABLE 15

*Trihybrid (Treating the gametes as units). Proportions of the different classes of gametes of generation n+1, in terms of those of the gametes of generation n.*

| GAMETES OF $n+1$ | | IN TERMS OF GAMETES OF $n$ |
|---|---|---|
| $q$ | = | $q(q+2r+s)$ |
| $r$ | = | $r(2q+3r+s)$ |
| $s$ | = | $s(3q+3r+s)$ |

### 3. *The tetrahybrid*

By application of the methods set forth for the di- and trihybrid, the problem of the results of eliminating all completely dominant zygotes in tetrahybrids may be solved. Only the essential data and results will be given. The number of groups of gametes with which we must now work is 4; let the proportions of these be designated $q$, $r$, $s$, and $t$ according as they contain respectively 3, 2, 1, and 0 dominant factors. The proportions

of these derived from generation $n+1$, expressed in terms of those derived from the previous generation $n$ are given in table 16.

TABLE 16

*Tetrahybrid (treating the gametes as units). Proportions of any class of gametes belonging to groups q, r, s, and t from generation n+1, in terms of those from generation n.*

| GAMETES OF GENERATION n+1 | | IN TERMS OF GAMETES OF GENERATION n |
|---|---|---|
| $q$ | = | $q(q+3r+3s+t)$ |
| $r$ | = | $r(2q+5r+4s+t)$ |
| $s$ | = | $s(3q+6r+4s+t)$ |
| $t$ | = | $t(4q+6r+4s+t)$ |

In the tetrahybrid the proportion of completely dominant zygotes (hence to be eliminated), in any generation is found to be in terms of the proportions of the gametes which produce them:

$$\frac{4q(3q+6r+2s)+6r^2}{(4q+6r+4s+t)^2} \tag{17}$$

### 4. *Polyhybrids for any number m pairs of allelomorphs*

Comparative consideration of results thus far reached with the di-, tri-, and tetrahybrids now puts us in a position to obtain by mathematical induction a general method for dealing with any polyhybrid, whatever the number of pairs of allelomorphs, thus yielding a general solution of our problem.

a. General formulæ for the proportions of the different types of gametes of any generation $n+1$, in terms of those of the previous generation $n$;

In any polyhybrid $AaBbCc\ldots$, heterozygous for all its $m$ pairs of allelomorphs, the number of different kinds of gametes produced is $2^m$. If these be grouped according to the number of dominant factors they contain, in order from $m$ dominants to 0, we find that they fall into $m+1$ groups, and the numbers of different gametes in each group are equal to the successive terms of the expanded binomial $(1+1)^m$. This has been illustrated for the trihybrid in table 12. When now these gametes mate among themselves at random, each kind mates with all the groups (table 12); the consequence is that in the next generation all fall again into the form of the expanded binomial $(1+1)^m$. In our problem, however, as we have seen, the first group (that containing $m$ dominants) does not occur after the first selection has occurred. This modifies the binomial series in definable ways, which may be discovered by comparing the gametic formulæ for the di-, tri-, and tetrahybrids given in tables 7, 15, and 16.

These formulæ give the proportions of the different types of gametes of any generation $n+1$, in terms of those of the previous generation $n$.

It is most instructive to compare first the formula for any gametic type ($r$) containing just $m-2$ dominants. These are (considering the gametes as fixed units):

TABLE 18
*Linkage Complete.*

| $m$ | GENERATION $n+1$ | GENERATION IN TERMS OF GENERATION $n$ |
|---|---|---|
| 2 | $r$ | $r(2q+r)$ |
| 3 | $r$ | $r(2q+3r+s)$ |
| 4 | $r$ | $r(2q+5r+4s+t)$ |

The expressions within the parentheses, at the right, consist of a set of terms that contain the series of gametes $q$, $r$, $s$, etc., (these being the designations for the gametes containing respectively $m-1$, $m-2$, $m-3 \ldots 0$, dominants), each with a coefficient. These coefficients show a relation to the expanded binomial $(1+1)^m$ that may be defined as follows. Each is the expansion of $(1+1)^m$, from which has been subtracted, beginning at the left, the terms of $(1+1)^{m-2}$. Thus to illustrate from the trihybrid $(m+3)$:

$$\begin{aligned} (1+1)^m &= 1p+3q+3r+1s \\ (1+1)^1 &= 1p+1q \end{aligned} \qquad (19)$$

Difference $2q+3r+1s$

Now, further comparison will show that this relation is general, the expansion to be subtracted being always $(1+1)^{m-k}$, where $m-k$ is the number of dominant factors in the gamete whose proportions are sought. Thus, for the gamete $r$, containing $m-2$ dominant factors, in the case of the tetrahybrid, we have

$$\begin{aligned} (1+1)^4 &= 1p+4q+6r+4s+1t \\ (1+1)^2 &= 1p+2q+1r \end{aligned} \qquad (20)$$

Difference $2q+5r+4s+1t$

Thus the coefficients are always given by the successive terms of $(1+1)^m-(1+1)^{m-k}$, the subtraction being at the left. We may therefore formulate as follows:

FORMULA 21

In any polyhybrid of $m$ pairs of allelomorphs:

Let the gametes containing respectively $m$, $m-1$, $m-2$, $m-3$, . . . . 0 dominant factors be designated by the series of letters $p$, $q$, $r$, $s$, $t$, . . . . $z$ (so that $r$ proportion of any type of gametes containing $m-2$ dominants, etc.).

Let $x$ represent algebraically any one of these types containing $m-k$ dominant facors.

Let $c_1$, $c_2$, $c_3$, $c_4$, etc., represent the respective coefficients of $p$, $q$, $r$, $s$, etc.

Then if all completely dominant zygotes are eliminated in each generation, the proportions of the gametes, if linkage were complete, of any type $x$, containing $m-k$ dominant factors, for any succeeding generation $n+1$, would be given in terms of the gametic proportions of the preceding generation $n$, by an expression of the form.

$$\begin{array}{ccc} \text{Generation } n+1 & & \text{Generation } n \\ x & = & x(c_2q+c_3r+c_4s \ldots . \text{ etc.}) \end{array} \qquad (21)$$

in which the successive values of the coefficients $c_2$, $c_3$, $c_4$, etc., are given by the terms of the series $(1+1)^m-(1+1)^{m-k}$ (the subtraction beginning at the left). The coefficient $c_1$ of course always disappears.

By the use of this general formula 21, the special formulæ for transforming the gametes of any generation $n$ into those of the succeeding generation $n+1$ can be at once written out for any polyhybrid.

Example. In a tetrahybrid, what is the formula for a gametic type $r$ containing just two dominants, (linkage complete) in terms of the gametes of the preceding generation? Here $m=4$, $k=2$, $m-k=2$. The coefficients are therefore given by $(1+1)^4-(1+1)^2$, and the formula is:

$$\begin{array}{ccc} \text{Generation } n+1 & & \text{Generation } n \\ r & = & r\,(2q+5r+4s+t) \end{array}$$

Similarly for the octahybrid, what is the formula for the gametic type $u$, containing just three dominants? Here $m=8$, $m-k=3$. The coefficients are given by $(1+1)^8-(1+1)^3$, so that the formula is:

$$\begin{array}{ccc} \text{Generation } n+1 & & \text{Generation } n \\ u & = & u(5q+25r+55s+70t+56u+28v+8w+x) \end{array}$$

We have now derived a general method for obtaining the gametes of generation $G_n+1$ in terms of the gametes of generation $G_n$ which holds as long as none of the combinations of gametes are heterozygous in more than a single pair of characters. We will now determine what modifications are necessary to make the method hold for all gametes regardless of the number of factors in which the combinations are heterozygous. To do this we must first consider the effects of this "shifting" or recombination of factors within the zygote, which results in the zygote producing gametes quite different from those from which it itself was formed.

It will be noted that as a result of the reduction division gametes are always produced in pairs. Either gamete may have all or none of the dominant factors (hence also recessive) of the zygote or any number of

the same; however, *the pair of gametes will together have exactly as many dominant and recessive factors as the parent zygote had.* It follows that no matter what gametes are produced from a zygote they will be produced in pairs and the two gametes of the pair will contain together just as many dominant and recessive factors as the gametes of any other pair. To illustrate: a pentahybrid zygote has four different dominant factors which are all heterozygous. Let it be represented thus *AaBbCcDdee.* There will be 16 different gametes produced which will all occur in pairs designated by our scheme as *qu, rt, ss.* As these pairs are the only ones which contain these particular factors, of necessity, the parent zygote was formed by the fusion of the members of one of these pairs. Thus the gametes of any one of these pairs in the $G_n$ generation produce all three pairs in generation $G_{n+1}$. Or stated conversely

$$qu_{n+1} = qu_n + rt_n + ss_n$$

and so on for each of the other pairs.

Pairs of gametes then function in groups. A pair whose sum of dominant factors in generation $G_{n+1}$ was, say $m-1$, is produced by all pairs which had $m-1$ dominants in generation $G_n$ and by no other pair.

Our method of designating the gametes by a symbol which stands for all gametes which contain a like number of dominant factors allows us to make a general statement covering all of this "shifting" of factors, so we can state exactly what gametes will be produced in generation $G_{n+1}$ from given gametes of generation $G_n$.

Let us take for example the zygotes of a generation of a pentahybr d. We will form the zygotes by crossing every gamete with itself and every other gamete, thus:

TABLE 22

| *p* | *q* | *r* | *s* | *s* | *et* | *pu* |
|---|---|---|---|---|---|---|
| *p* | *q* | *pq* | *pr* | *s* | *pt* | *qu* |
| *q* | *qp* | *qq* | *qr* | *qs** | *qt** | *qu** |
| *r* | *rp* | *rq* | *rr** | *rs** | *rt** | *ru** |
| *s* | *sp* | *sq** | *sr** | *ss** | *st** | *su** |
| *t* | *tp* | *tq** | *tr** | *ts** | *tt** | *tu* |
| *u* | *up* | *uq** | *ur** | *us** | *ut* | *uu* |

Ignoring all zygotes containing *p* as a factor, for according to our scheme of selection no gametes containing all *m* dominants (*p*) are produced, if we mark all zygotes with an asterisk as shown above, each line of asterisks will cross all pairs of gametes which contain an equal number of dominant factors, and hence each pair will produce in the next generation all of the gametes on the line which crosses it, paired as they are in

the diagram, and produce no other gametes. Starting with the pair which contains the greatest number of dominants the groups are:

| NO. OF DOMINANT FACTORS IN ZYGOTE | PAIR OF GAMETES PRODUCED | |
|---|---|---|
| 2 (m−1) | *qq* | |
| 2 (m−1)−1 | *qr*, *rq* | |
| 2 (m−1)−2 | *qs*, *rr*, *sq* | |
| 2 (m−1)−3 | *qt*, *rs*, *sr*, *tq* | |
| 2 (m−1)−4 | *qu*, *rt*, *ss*, *tr*, *uq* | (23) |
| 2 (m−1)−5 | *ru*, *st*, *ts*, *ur* | |
| 2 (m−1)−6 | *su*, *tt*, *us*. | |
| 2 (m−1)−7 | *tu*, *ut* | |
| 2 (m−1)−8 | *uu*. | |

The above can be simplified by combining the like pairs. Thus as $qr = rq$ they can both be written either as one or the other.

We have now determined which gametes are produced in the $G_{n+1}$ generation from a given pair of gametes in generation $G_n$. The next point to be settled is in what proportion are the various gametes produced?

First, when a pair of like $G_n$ gametes produce a homozygous zygote, all of the gametes produced in $G_{n+1}$ are, of course, identical and the same as the gametes $G_n$. This is the case with all zygotes which have 2 $(m-1)$ dominant factors paired as they are in the diagram. Second, when a pair of $G_n$ gametes produce a zygote heterozygous for only one factor there are only 2 kinds of gametes produced in the $G_{n+1}$ generation and these are produced in equal numbers and are identical with the two $G_n$ gametes. This is the case with all zygotes which have 2 $(m-1)-1$ dominant factors. Third, when a pair of $G_n$ gametes produce a zygote heterozygous for two factors, the case is more complicated, for here 4 different gametes are produced in generation $G_{n+1}$ only 2 of which were present in the direct line in generation $G_n$. For example the zygote *AABbCcdd* will produce four gametes paired as follows:

$$\left\{\frac{ABCc}{Abcd}\right\} \quad \left\{\frac{ABcd}{AbCd}\right\} \quad \left\{\frac{AbCd}{ABcd}\right\} \quad \left\{\frac{Abcd}{ABCd}\right\}$$

According to our scheme these would be written *qs*, 2*rr*, *sq*. As the different pairs of gametes are produced in equal numbers the number of a particular gamete produced by all such zygotes is ¼ of the number of such pairs produced. For example

$$q_{n+1} = \frac{q_n s_n + 2r_n r_n + s_n q_n}{4}$$

Fourth, when a zygote produced by a pair of $G_n$ gametes is heterozygous in regard to these factors, eight $G_{n+1}$ gametes are produced. Thus the zygote *AaBbCcdd* produces the following pairs of gametes:

$$\left\{\frac{ABCd}{abcd}\right\}\left\{\frac{ABcd}{abCd}\right\}\left\{\frac{AbCd}{aBcd}\right\}\left\{\frac{aBCd}{Abcd}\right\}\left\{\frac{Abcd}{aBcd}\right\}\left\{\frac{aBcd}{AbCd}\right\}\left\{\frac{abCd}{ABcd}\right\}\left\{\frac{abcd}{ABcd}\right\}$$

These would be represented:

$$qt,\ 3rs,\ 3sr,\ tq$$

The relative number of a given gamete in generation $G_{m+1}$ would be 1/8 of the total number of such zygotes. For example:

$$q_{m+1}=\frac{q_nt_n+3r_ns_n+3s_nr_n+t_nq_n}{8}$$

Fifth, when a zygote is heterozygous for four factors, sixteen different gametes are produced. They are represented by

$$qu,\ 4rt,\ 6ss,\ 4tr,\ uq.$$

Each gamete would be 1/16 of the total. Thus

$$q_{m+1}=\frac{q_nu_n+4r_nt_n+6s_ns_n+4t_nr_n+u_nq_n}{16}$$

We can now state the above cases in a general form. Let $h$ = the number of heterozygous factors in a zygote. Then the number of any gamete $g$ produced by any zygote would be expressed

$$g=\frac{(1+1)^h}{2^h}$$

where the expanded form of the numerator would give the coefficients of the pairs of gametes in the order of their occurrence in table 22. A further step in simplification can be taken by combining like pairs and cancelling factors that occur in both numerator and denominator. To illustrate:

TABLE 24

| VALUES OF $h$ | $G_{n+1}$ GAMETES | ZYGOTES IN TERMS OF $G_n$ GAMETES | SIMPLIFIED $G_n$ GAMETES |
|---|---|---|---|
| 1 | $q_{n+1}$ = | $\frac{q_nr_n+r_nq_n}{2}$ | = $q_nr_n$ |
| 2 | $q_{n+1}$ = | $\frac{q_nr_n+2s_ns_n+r_nq_n}{4}$ | = $\frac{q_nr_n+s^2_n}{2}$ |
| 3 | $q_{n+1}$ = | $\frac{q_nt_n+3r_ns_n+3s_nr_n+tXqX}{8}$ | = $\frac{q_nr_n+3r_ns_n}{4}$ |
| 4 | $q_{n+1}$ = | $\frac{q_nu_n+4r_nt_n+6s_ns_n+4t_nr_n+u_nq_n}{16}$ | = $\frac{q_nt_n+4r_nt_n+3s^2_n}{8}$ |

According to our scheme of selection the maximum value of $h$ is $m-1$. The value of $h$ increases from 0 in zygotes which have 2 $(m-1)$ dominants to $m-1$ in zygotes of $m-1$ dominants and then decreases as the number of dominants decreases until it is again 0 in zygotes which have $m-m$ dominants.

In the pentahybrid another factor, which will be treated later, occurs which concerns this "shifting" of gametes in the gamete pairs $rt$, $ss$, and $tr$.

We have now determined which pairs of gametes participate in every particular "shifting" of gametes from generation to generation and also what proportion of the various gametes are produced from each "shift." One more factor must be evaluated before this "shifting," which we will now call "primary shifting" for reasons which will appear later, will be completely solved. As has been stated before, we designated all gametes with an equal number of dominant factors with the same symbol. For example, in the pentahybrid there are 5 different gametes designated by $q$, 10 designated by $r$, and 10 designated by $s$. A given gamete, say $q$ combined with $s$, would produce a zygote quite different from some other cross of $q$ and $s$. The only thing all crosses of $q$ and $s$ would have in common would be the total number of dominant (also recessive) factors. They would differ considerably in regard to the number of heterozygous factors. If $10r$ crosses with $10s$ the result will be $100rs$. How many of these 100 combinations will be heterozygous for 1 factor and how many for 3 factors? (Those heterozygous for 5 factors would possess all 5 dominants and would be eliminated). Or, when we cross $10r$ with itself how many combinations are homozygous, and hence are not subject to this gamete "shifting" and how many are heterozygous for 2 factors and are subject to the shifting? (Those heterozygous for 4 factors would contain all $m$ dominants and would be eliminated.) A very simple method of answering this question has been derived empirically. The pentahybrid will be used throughout as an illustration.

First, when any gamete is combined with a gamete which has $m-m$ or 0 dominant factors all of the resultant combinations of gametes are heterozygous for each and every dominant factor which they contain. This gives us for the coefficients of the "shifts" in the last line of our table, all except the first term of the expanded binomial $(1+1)^m$, and gives us $u_{n+1}$ in terms of $u_n$. (See formula 21.) Thus, in the pentahybrid:

$$u_{n+1}=\frac{5(q_nu_n+4r_nt_n+3s_n{s_n}^2)}{8}+\frac{10(r_nu_n+3s_nt_n)}{4}+\frac{10(s_nu_n+{t_n}^2)}{2}+5t_nu_n+{u_n}^2$$

In a like manner the various combinations which contain $q$ can be

derived. The coefficients of the zygotes containing $q$ which are allowed to breed according to our scheme of selection (formula 21) are the successive term of $(1+1)^m-(1+1)^{m-1}$ which equals $(1+1)^{m-1}$. Now all pairs must be homozygous recessives in regard to 1 factor (otherwise they would be eliminated), and consequently any gamete so paired with $q$ that the resultant zygote be allowed to reproduce will be heterozygous for *1* less than the number of recessives such a gamete had. This is true of the matings of all of the 5 gametes designated $q$. Consequently this same "shifting" occurs in all of the gametes labeled $q$. Thus in the pentahybrid (table 21),

$$q_{n+1}=q_n{}^2+4qr_n+\frac{6qs_nr^2}{2}+\frac{4(qt_n+3rs_n)}{4}+\frac{1(qu_n+4rt_n+3s_n{}^2)}{8}$$

It must be remembered that in our table for squaring the sum of the gametes that each combination of gametes occurs twice, that since $qu=uq$, the number of "shifts" must be the same for both places. We have solved the problem of this shifting for all combinations of $q$ with all other gametes and of $n$ with all other gametes. We may now unite this much of the table for squaring the sum of the gametes. The numbers being only the coefficients of the gamete pairs in which this primary "shifting" takes place.

TABLE 25

*Pentahybrid.*

| | | $q$ | $r$ | $s$ | $t$ | $u$ |
|---|---|---|---|---|---|---|
| $5\ q_{n+1}$ | $=\ 5q$ | [1 | +4 | +6 | +4 | +1] |
| $10\ r_{n+1}$ | $=\ 10r$ | [2 | + | + | + | 1] |
| $10\ s_{n+1}$ | $=\ 10s$ | [3 | + | + | + | 1] |
| $5\ t_{n+1}$ | $=\ 5t$ | [4 | + | + | + | 1] |
| $u_{n+1}$ | $=\ 1u$ | [5 | +10 | +10 | +5 | +1] |

The coefficients in bold face type are those of zygotes homozygous and heterozygous for only 1 factor, consequently no shifting occurs in these cases.

Actual count has shown that,—*the number of gamete pairs in which "shifting" occurs, designated by a given pair of symbols, is, compared with the other pairs which participate in the "shift," proportional to the relative number of such pairs produced by the "shift" in question.* To illustrate: In the "shift" which occurs in the pairs heterozygous for 2 factors (containing 2 $(m-1)-2$ dominant factors) designated $qs$ and $r^2$, the relation of $qs$ to $r^2$ is 1 : 1, $(qs+r^2)/2$, consequently there must be as many pairs of $r^2$ gametes as there are $qs$ gametes. There are in the table 60 gametes designated $qs$, $(5q\times 6s+10s\times 3q)$, and consequently there must be 60 $r^2$ gametes. One of the factors of the 60 gametes is known, that is,

$10r$, (table 25), the other must be $6r$, $(60r^2/10r = 6r)$, and the coefficient of the $r^2$ pair in the table must be 6 (table 25). Likewise for the "shift" in those pairs heterozygous for 3 factors. Here the relation of $qt$ to $rs$ is 1 : 3, $(qt+3rs)/4$, hence there must be three times as many pairs designated $rs$ in which this shift occurs as pairs designated $qt$. The number of such $qt$ pairs is 40, $(5q \times 4t + 5t \times 4q)$, hence there must be 120 pairs of gametes labeled $rs$. These fall into 2 equal groups $(rs = sr)$ of 60 each. One factor of each group is known, $10r$ and $10s$, the other factors must consequently be $6s$ and $6r$ (table 25). The coefficients for the pair of gametes heterozygous in regard to 4 factors which participate in this shifting are derived in the same way. Here the proportion of $qu$ to $rt$ to $s^2$ is 1 : 4 : 3, $(qu+4rt+3s^2)/8$, hence since there are 10 pairs of $qu$ "shifting" there must be 40 pairs of $rt$ and 30 of $sr$. Solving for the coefficients in the table as we did for the other 2 "shifts" we get them to be $1qr$, $2rt$, $3s^2$, $4tr$, $5uq$.

Completing the table we get:

TABLE 26

| | $q$ | $r$ | $s$ | $t$ | $u$ |
|---|---|---|---|---|---|
| $5q_{n+1} = 5q_n$ | (1 | + 4 | + 6 | + 4 | + 1) |
| $10r_{n+1} = 10r_n$ | (2 | + 6 | + 6 | + 2 | + 1) |
| $10S_{n+1} = 10S_n$ | (3 | + 6 | + 3 | + 3 | + 1) |
| $5t_{n+1} = 5t_n$ | (4 | + 4 | + 6 | + 4 | + 1) |
| $u_{n+1} = u_n$ | (5 | +10 | +10 | + 5 | + 1) |

An examination of the above table reveals a number of series which can be used as a check upon the accuracy with which the coefficients in question have been derived. If we draw a diagonal line from the upper right hand corner to the lower left the numbers crossed will be 1, 2, 3, 4, . . . . $m$. All of the coefficients to the right of and including this line and below it form all except the first term of the expanded binomial $(1+1)^r$, when $r$ equals the number of recessive factors in the gamete of generation $G_{n+1}$ which is being derived from the pairs on that line. Thus then the number of recessives in $t_{n+1}$ is 4, and the coefficients in the next to the last line to the right of and including the diagonal are all except the first term of the expanded binomial $(1+1)^4$. The coefficients to the left of and above this diagonal, also including it, likewise form series. They are the successive terms of the expanded form of $r\ (1+1)^{m-r}$, $r$ being equal to the number of recessives in the gamete in question. Thus the coefficients of the first line are 1 $(1+1)^{m-1}$ of the second line 2 $(1+1)^{m-2}$ of the third line 3 $(1+1)^{m-3}$, etc. There are any number of other series which can also be used as checks. The problem of the effects of this "primary shifting" is thus completely solved.

There now remains only the necessity of combining our various results to enable us to state the value of a gamete in terms of the gametes of the preceding generation. Thus in the case of the tetrahybrid, if there were no "shifting" $r_{n+1}$ would equal $r_n(2q_n+5r+4s_n+t_n)$ but since shifting would occur in 4 of the pairs designated $r^2$, 2 of those designated $rs$ and 1 of those designated $rt$, it would be necessary to subtract these from the total number of pairs to derive the number of pairs in which shifting did not occur. By adding the sum of the pairs in which "shifting" does not occur to the sum of the various "shifting" pairs the value of $r_{n+1}$ is obtained thus:

$$r_{n+1}=2r_nq_n+[r_n^2+\frac{4(q_ns_n+r_n^2)}{2}]+[2r_ns_n+\frac{2(q_nt_n+3r_ns_n)}{4}]+\frac{(r_nt_n+s_n^2)}{2}$$

(2) (5) (4) (1)

The numbers in parentheses on the lower line are equal to the sum of the coefficients of each of the terms of the above equations and are equal to the coefficients of the terms of the corresponding equations in formula 21.

As we have previously mentioned, another factor enters into the "shifting" of the gamete pairs in the pentahybrid. Some of the pairs, $qu$, $rt$, and $s^2$, are heterozygous for 4 factors. This causes a "primary shifting" which has been solved. In addition certain of these pairs of $rt$ and $s^2$ are heterozygous for 2 factors, and consequently there enters here into our formulæ a "secondary shifting," the effects of which can be evaluated exactly as those of the "primary shifting."

It is to be noted, first, that all of the zygotes produced by gamete-pairs designated $qu$ are heterozygous for 4 factors and consequently are not affected by this "secondary shift." Second, all of those produced from pairs $rt$ and $s^2$ which are not heterozygous for 4 factors are heterozygous for *2* except a single pair of those designated $s^2$, which is homozygous; these, heterozygous for 2 pairs of factors, do participate in the "secondary shift." The number of times this secondary shift occurs can thus be easily obtained by subtracting the exponents of the pairs which undergo the "primary shift" (table 26) formed from the total number of pairs designated by the same symbols (table 15). The result will give the exponents of those which undergo this "secondary shifting." It must be remembered, however, that every time a gamete is paired with those of the group to which it belongs, such combinations being represented by $r^2$, $s^2$, $t^2$, etc., a single combination results which is completely homozygous and hence does not "shift" at all. In the hexahybrid certain of the pairs

*ru*, *st*, and *sv* and $t^2$ experience this "secondary shift," *ru* and *st* being heterozygous for 5 and 3 factors and *sv* and $t^2$ for 4 and 2. This "second shift" is exactly similar to the first. When the pairs are heterozygous for 2 factors the shift is expressed $(rt+s^2)/2$ or $(sv+t^2)/2$, when they are heterozygous for 3 factors it is expressed $(ru+3st)/4$. To illustrate: the total number of the pair *ru* in the hexahybrid is 6 (table 21). The number of times the pair *ru* participates in the primary shift is 2. Consequently the number which participates in the secondary shift is 4. We have thus derived the coefficient for the first pair of all the groups which participate in the "secondary shifting." If we know this coefficient the other coefficients are easily obtainable, for here as in the primary shifting, *the relative numbers of the pairs which participate in the shift are proportional to the numbers of such pairs produced by the shift in question.* Thus if in the hexahybrid the number of *ru's* which participate in the shift is 120, $(4u\times15r+10r\times6u)$, the number of *st's* will be 360, $(ru+3st)/4$ ratio 1 : 3, and thus their coefficients in the table, derived exactly as in the "primary shift" must be 9 and 12. The group of coefficients is then 4 (*ru*), 9 (*st*), 12 (*ts*) and 10 (*ur*).

TABLE 27

*Coefficients of the pairs participating in the "secondary shift".*

PENTAHYBRID

| | *q* | *r* | *s* | *t* | *u* |
|---|---|---|---|---|---|
| 5*q* | | | | | |
| 10*r* | | | | +3 | |
| 10*s* | | | +6 | | |
| 5*t* | | +6 | | | |
| *u* | | | | | |

HEXAHYBRID

| | *q* | *r* | *s* | *t* | *u* | *v* |
|---|---|---|---|---|---|---|
| 6*q* | | | | | | |
| 15*r* | | | | | 6 + 4 | |
| 20*s* | | | | 9 + 9 + 3 | | |
| 15*t* | | | 6 +12 + 8 | | | |
| 6*u* | | | 10 +10 | | | |
| *v* | | | | | | |

In the heptahybrid still another "shift" appears, a "tertiary shift." It occurs in those gamete groups where a single set of symbols will represent combinations of gametes heterozygous for 6, 4 and 2 factors. Those combinations heterozygous for 6 factors are handled in the "primary shift," those heterozygous for 4 pairs in the "secondary" and those heterozygous for 2 pairs in the "tertiary." Thus in each of the pairs symbolized by *qw*, *rv*, *su* and $t^2$ there are pairs heterozygous for 6 factors;

in *rv*, *su* and $t^2$ are those heterozygous for 4 factors; and in *su* and $t^2$ are those heterozygous for 2 factors. The coefficients of the pairs participating in this "tertiary shift" are found exactly as those for the "secondary." In the third pair of symbols *su* all of the pairs that are not heterozygous for 6 factors and 4 factors are heterozygous for 2 factors (except, of course, a single homozygous combination represented by $t^2$), and thus participate in this tertiary shift. By adding in the "primary shift" to those of "secondary shift" and subtracting their sum from the total number of such pairs, we get the number which participate in the "tertiary." Knowing the coefficient of the first numbers of a group of pairs participating in a particular shift we can easily obtain the coefficients of the other pairs involved by the method used in the primary and secondary shifts. For the heptahybrid the coefficients of those pairs participating in the tertiary shift are:

TABLE 28

| | *q* | *r* | *s* | *t* | *u* | *v* | *w* |
|---|---|---|---|---|---|---|---|
| 7*q* | | | | | | | |
| 21*r* | | | | | | | |
| 35*s* | | | | | +6 | | |
| 35*t* | | | | +12 | | | |
| 21*u* | | | +10 | | | | |
| 7*v* | | | | | | | |
| 1*w* | | | | | | | |

Of course this "tertiary shifting" is present in all hybrids higher than the heptahybrid, and in the nonahybrid a "quarternary shifting" appears. In every higher hybrid where *m* is odd, a new order of shifting appears. However the increasing cumbersomeness of the equations makes it futile to extend this method of calculating the composition of gametes $G_{n+1}$ in terms of those of $G_n$.

To determine numerical values, since we begin with the complete $F_1$ heterozygote *AaBbCc* etc., the value of each class of gametes at the commencement is 1: employing successively for one generation at a time the above formula 21, we may determine the proportions for each class of gametes after any number of generations. The proportion of completely dominant zygotes produced from these may then be determined, by the methods to be taken up next.

b. Determination of the proportion of completely dominant zygotes, to be obtained from the gametes of any generation: The total number of zygotes produced by the random mating of any set of gametes is given by squaring the numbers representing the gametes (since each kind of gamete mates in equal numbers with each kind). After we have found the pro-

portions of each type of gamete $p$, $q$, $r$, $s$, $t$, etc., for the given generation $(n+1)$, the total number of gametes will be given by an expression made up in accordance with the following:

(1) The class of gametes $p$, in which all $m$ factors are dominant, does not appear at all.

(2) Of the other classes, containing $m-1$, $m-2$, etc., dominants, none disappear, and all those containing the same number of dominants are present in equal number.

(3) Hence we have present all possible classes of gametes producible by the polyhybrid of $m$ pairs of allelomorphs, except that containing $m$ dominants. All possible classes are represented, as we have seen, by the expansion of $(1+1)^m$ (see table 12). All possible classes except the first, containing $m$ dominants, will therefore be represented by the expansion of $(1+1)^m$, when this is deprived of its first term. Thus, in the pentahybrid, the gametes will be represented by the expression

$$5q+10r+10s+5t+1u$$

(The diversities in proportions are expressed in the values to be given to $q$, $r$, $s$, etc., not in their coefficients.)

The zygotes of the next generation are produced by the random mating of these; and their number is to be represented by the square of the expression just given. In general, the total number of zygotes of any generation is expressible in terms of the gametes from which they are produced, as follows:

In any polyhybrid of $m$ allelomorphs—

Let $p$, $q$, $r$, $s$, etc., represent respectively the proportions of the types of gametes containing $m$, $m-1$, $m-2$, $m-3$, etc., dominant factors.

Let $c_1$, $c_2$, $c_3$, be the respective coefficients of these types of gametes.

Then the total number of zygotes is given by the expression:

$$(c_2q+c_3r+c_4s \cdots \text{to } m \text{ terms})^2 \qquad (29)$$

in which the successive coefficients $c_2$, $c_3$, etc., are given by the successive terms, omitting the first of the expansion of $(1+1)^m$.

We require further to know what proportion of these zygotes will be dominant for the entire $m$ pairs of factors (and are hence to be eliminated). We can obtain a general formula for this by induction from the results for the di-, tri-, and tetrahybrid. Brief formulæ for these results are given in formulæ 8, 14, and 17, but for the present purposes it will be necessary to examine in detail the methods by which the formulæ are obtained, and express them in a more general form.

The total number of zygotes of all kinds obtainable from the gametes of a given generation is expressed by squaring the expression for the

gametes, as in formula 29. Each kind of gamete is crossed with every other kind, in numbers proportional to the relative numbers of each kind present. To determine which of the resulting combinations will be dominant for all the $m$ factors, the different kinds of gametes must be dealt with individually, since, when a gamete having say two dominant factors is mated with a gamete having say three dominant factors, it depends upon the precise constitution of each whether the results are entirely dominant or not. For example, $Abcd \times aBCD$ gives a completely dominant zygote, while $ABcd \times ABCd$ does not. However, it is sufficient to examine the results for the diverse matings of any typical gamete for any group (as the group $r$, containing two dominant factors), for any other gametes of that group the results will be the same (when we begin as in the present study, with all kinds of gametes in equal numbers).

Proceeding to such an examination, it is to be recalled that the gamete $p$ (containing $m$ dominant factors) does not appear (after $G_1$). For the dihybrid there remains in any generation only the set of gametes represented by $2q+r$. Mating each of these with each other, we find that completely dominant zygotes (containing $AB$) are given simply by $2q^2$, which may be written for our purposes

$$2q\ (q)$$

In the trihybrid, the gametes of which are represented in any generation by $3q+3r+s$, matings show that completely dominant zygotes are given by the following:

$$3q\ (2q+r)$$
$$3r\ (q)$$

And in the tetrahybrid completely dominant zygotes are produced by the mating of gametes which we represent as follows:

$$4q\ (3q+3+s)$$
$$6r\ (2q+r)$$
$$4s\ (q)$$

The law of formation of these expressions is obvious on inspection, so that one can readily write them out for higher polyhybrids. The pentahybrid, for example, evidently yields for the completely dominant zygotes:

$$\begin{aligned} &5q\ (4q+6r+4s+t) \\ +&10q\ (3q+3r+s) \\ +&10r\ (2q+r) \\ +&\ 5s\ (q) \end{aligned}$$

For a hybrid of $m$ allelomorphs, the sum of the completely dominant zygotes is given by the sum of $m-1$ expressions, each of which consists of a quantity outside the parenthesis and a quantity within it. The $m-1$ quantities outside the parenthesis are successively $c_2q$, $c_3r$, $c_4s$, etc., in which the coefficients $c_2$, $c_3$, etc., are respectively the second, third, fourth, and succeeding terms of the expansion of $(1+1)^m$. The quantities within the parentheses are $c_2q\ c_3r\ c_4s$, and so on, the coefficients for the first parenthesis being given by all but the first term of $(1+1)^{m-1}$, those for the second term by all but the first term of $(1+1)^{m-2}$, and so on, the coefficient of the last parenthesis being given by $(1+1)^0$, so that it is 1.

Since the $k$ term of $(1+1)^m$ is $m!/(k-1\ !m-(k-1)!)$, we can write a general formula for the sum of the completely dominant zygotes, in terms of the gametes from which they are derived. This divided by the expression given in formula 29 will give the actual proportion in any generation that the completely dominant zygotes are of the whole. This formula for the proportions is as follows:

FORMULA 30

*Proportions of the entire set of zygotes that are completely dominant, in any generation, in terms of the gametes from which they are derived, for any polyhybrid of m pairs of allelomorphs, when the completely dominant zygotes have been eliminated throughout the preceding generations. The numerator is the sum of m−1 expressions, constituted as follows:*

$$\frac{m}{1!m-1!}q\frac{m-1!}{1!m-2!}q\frac{m-1!}{2!m-3!}p\frac{m-1!}{3!m-4!}s+\cdots \text{ to } m-1 \text{ terms}$$

$$\frac{m}{2!m-2!}p\frac{m-2!}{1!m-3!}q\frac{m-2!}{2!m-4!}r+\cdots \text{ to } m-2 \text{ terms}$$

$$\frac{m!}{3!m-3!}s\frac{m-3!}{1!m-4!}q\frac{m-3!}{2!m-5!}r+\cdots \text{ to } m-3 \text{ terms}$$

and so on until there are $m-1$ such expressions.

The denominator is:

$$(c_2q+c_3r+c_4s\cdots, \text{ to } m \text{ terms})^2,$$

in which the successive coefficients $c_2$, $c_3$, $c_4$, etc., are given by the successive terms, *omitting the first, or* $c_1$, of the expansion of $(1+1)^m$.

Thus to determine for any polyhybrid of $m$ pairs of allelomorphs the proportion of completely dominant zygotes present in the successive generations, when all these are eliminated from each generation as they appear, one begins with each of the $m-1$ classes of gametes $o, p, q, r, s, t,$ etc., of $G_1$ in the proportion 1. These are then transformed into the gametic proportions of the succeeding generations by the method given.

Then for each generation the proportion of completely dominant zygotes is determined by the use of formula 30. Curves for the various polyhybrids up to $m=4$, thus determined, are given in Part V of this paper.

## PART II.

### THE ELIMINATION IN EACH GENERATION OF ALL INDIVIDUALS WHO ARE NOT DOMINANT FOR ALL OF THE $m$ INDEPENDENT FACTORS IN A POLYHYBRID OF $m$ ALLELOMORPHS

This problem is the complement of the one treated in Part I. If, in Part I, we were eliminating a character due to the simultaneous presence of $m$ dominant genes, we are here breeding for that character and selecting out all individuals who do not possess it, that is, all individuals who show any recessive traits. The method of deriving the equations, which show the effect of successive elimination each generation of all undesirable characters, is the same one used in Part I. Equations are derived for the simpler hybrids and, from them are obtained the underlying fundamental series which make it possible through mathematical induction, to obtain equations for all hybrids.

As we are here selecting out the recessives we may use the monohybrid as the simplest case. We could not do this when we were eliminating dominants, for the single elimination of a dominant from a monohybrid leaves the strain homozygous-recessive and the curve of the appearance of dominants reaches zero in the $F_3$ generation. The recessive, however, cannot be eliminated by any finite number of selections, as was shown by JENNINGS (1916), who derived a formula for its occurrence when it is not allowed to reproduce. The formula is

$$\frac{1}{(n+2)^2}$$

where $n$ equals the number of selections. In the present paper $n$ is used as the number of the filial generation, beginning with the parental cross $AA$ by $aa$, and with this value of $n$ the formula would be

$$\frac{1}{n^2}$$

This formula is the starting point of a series which solve all cases. It was possible to carry the formulæ much further than those derived in Part I. Instead of having to derive the gametes of a given generation in terms of the gamete of the preceding generation and repeating the performance for each generation until the desired generation is reached, we can here reduce the formulæ to two factors, $m$, the number of allelomorphs, and $n$ the number of the filial generation.

### 1. *The dihybrid*

The problem of the results of eliminating in each generation all of the individuals of a dihybrid stock who have one or more recessive traits, is attached by first deriving a method for expressing the gametes of the $n+1$ generation ($G_{n+1}$) in terms of the gametes of the $n$th generation ($G_n$). The necessary formulæ can be derived from tables 1 and 8. They are:

$$p_{n+1} = {}_n{}^2p + 2p_nq_n + \frac{p_nr_n + q_n{}^2}{2}$$

$$q_{n+1} = p_nr_n + \frac{p_nr_n + q_n{}^2}{2}$$

$$r_{n+1} = \frac{p_nr_n + q_n{}^2}{2}$$

Starting in the $G_1$ generation with $p$, $q$, and $r$ each equalling 1, we get upon simpification:

TABLE 31

| | $G_1$ | $G_2$ | $G_3$ | $G_4$ | $G_5$ | $G_6$ | $G_n$ |
|---|---|---|---|---|---|---|---|
| $p$ = | 1 | 4 | 9 | 16 | 25 | 36 | $n^2$ |
| $q$ = | 1 | 2 | 6 | 4 | 5 | 6 | $n^1$ |
| $r$ = | 1 | 1 | 1 | 1 | 1 | 1 | $n^0$ or 1 |

The formula for deriving the percentage of zygotes containing some recessive characters from a given set of gametes is: (see tables 8 and 30)

$$\frac{2q^2 + 4qr + r^2}{(p + 2q + r)^2}$$

Substituting in the above for $p$, $q$, and $r$ their values in terms of any given generation $G_n$, $p = n^2$, $q = n$, $r = n$ or 1, we get

$$= \frac{2n^2 + 4_n + 1}{(n+1)^4}$$

Simplifying

$$=\frac{2(n^2+2n+1)-1}{(n+1)^4}$$

$$=\frac{2(n+1)^2}{(n+1)^4}-\frac{1}{(n+1)^4}$$

$$=\frac{2}{(n+1)^2}-\frac{1}{(n+1)^4}$$

Now expressing our formula, at present in terms of the gametes of $G_n$ generation, in terms of $F_n$ ($G_n$ producing $F_{n+1}$), we get for the proportion of zygotes in any generation that are not completely dominant (and are hence to be eliminated from the parents of the next generation)

$$\frac{2}{n^2}-\frac{1}{n^4}$$

As $n$ increases, the value of the second term of our formula so decreases in proportion to the first term that it can be omitted without altering to any appreciable extent the value of the formula when $n$ is large. When $n=10$ the value of the second term is only 1/2 percent of the first.

### 2. *The trihybrid*

The problem of the results of eliminating from a trihybrid stock all individuals who are not dominant for all three allelomorphs is attacked precisely as in the case of the dihybrid. The formulæ for expressing the gametes of the $n+1$ generation in terms of those of the $n$th generation are:

$$p_{n+1}=p_n^2+3p_nq_n+3\frac{p_nr_n+q_n^2}{2}+\frac{p_ns_n+3q_nr_n}{4}$$

$$q_{n+1}=p_nq_n+2\frac{p_nr_n+q_n^2}{4}+\frac{p_ns_n+3q_nr_n}{4}$$

$$r_{n+1}=\frac{p_nr_n+q_n^2}{2}+\frac{p_ns_n+3q_nr_n}{4}$$

$$s_{n+1}=\frac{p_ns_n+3q_nr_n}{4}$$

As $p$, $q$, $r$, and $s$ equal 1 in the $G_1$ generation, substituting in the formulæ we get their numerical values to be:

| | $G_1$ | $G_2$ | $G_3$ | $G_4$ | $G_n$ |
|---|---|---|---|---|---|
| $p_1$ | 1 | 8 | 27 | 64 | $n^3$ |
| $q_1$ | 1 | 4 | 9 | 16 | $n^2$ |
| $r_1$ | 1 | 2 | 3 | 4 | $n^1$ |
| $s_1$ | 1 | 1 | 1 | 1 | $n^0$ or 1 |

The corresponding formulæ for deriving the percentage of individuals to be eliminated from a given group of gametes is:

$$\frac{3q(q+4r+2s)+3r(3r+2s)+s^2}{(p+3q+3r+s)^2}$$

Substituting for $p$, $q$, $r$, and $s$ in value in terms of $n$, the formula is

$$=\frac{3n^4+12n^3+15n^2+6n+1}{(n+1)^6}$$

Simplifying

$$=\frac{3(n+1)^4}{(n+1)^6}-\frac{3n^2+6n+2}{(n+1)^6}$$

$$=\frac{3}{(n+1)^2}-\frac{3(n+1)^2}{(n+1)^6}+\frac{1}{(n-1)^6}$$

$$=\frac{3}{(n-1)^2}-\frac{3}{(n+1)^2}+\frac{1}{(n+1)^6}$$

Expressing the above in terms of $F_n$, we get the proportion of zygotes still containing some recessive characters in the $n$th generation,

$$\frac{3}{n^2}-\frac{3}{n^4}+\frac{1}{n^6}$$

### 3. *The tetrahybrid*

The results of eliminating any and all recessives from a polyhybrid stock are obtained exactly as in the di- and trihybrids. The $G_{n+1}$ gametes expressed in terms of $G_n$ gametes are

$$p_{n+1}=p_n{}^2+4p_nq_n+6\frac{p_nr_n+q_n{}^2}{2}+4\frac{p_ns_n+3q_nr_n}{4}+\frac{p_nt_n+4q_ns_n+3r^2{}_n}{8}$$

$$q_{n+1}=p_nq_n+3\frac{p_nr_n+q_n{}^2}{2}+4\frac{p_ns_n+3q_nr_n}{4}+\frac{p_nt_n+4q_ns_n+3r_n{}^2}{8}$$

$$r_{n+1}=\frac{p_nr_n+q_n{}^2}{2}+2\frac{p_ns_n+3q_nr_n}{4}+\frac{p_nt_n+4q_ns_n+3r_n{}^2}{8}$$

$$s_{n+1}=\frac{p_ns_n+3q_nr_n}{4}+\frac{p_nt_n+4q_n+3r_n{}^2}{8}$$

$$t_{n+1}=\frac{p_nt_n+4q_ns_n+3r_n{}^2}{8}$$

The numerical values of the gametes, derived as in the di- and trihybrids are:

TABLE 32

| | $G_1$ | $G_2$ | $G_3$ | $G_4$ | $G_n$ |
|---|---|---|---|---|---|
| $p$ = | 1 | 16 | 81 | 256 | $n^4$ |
| $q$ = | 1 | 8 | 27 | 64 | $n^3$ |
| $r$ = | 1 | 4 | 9 | 16 | $n^2$ |
| $s$ = | 1 | 2 | 3 | 4 | $n^1$ |
| $t$ = | 1 | 1 | 1 | 1 | $n^0$ |

The formula for obtaining the percentage of zygotes which have some recessive characters is:

$$\frac{4q(q+6r+6s+2t)+6r(5r+8s+2t)+8s(2s+t)+t^2}{(p+4q+6r+4s+t)^2}$$

Expressed in gametes in terms of generation $G_n$:

$$\frac{4n^6+24n^5+54n^4+56n^3+28n^2+8n+1}{(n+1)^6}$$

Simplifying:

$$=\frac{4(n+1)^6}{(n+1)^6}-\frac{6n^4+24n^3+32n^2+16n+3}{(n+1)^6}$$

$$=\frac{4}{(n+1)^2}-\frac{6(n+1)^4}{(n+1)^6}+\frac{4n^2+8n-3}{(n+1)^6}$$

$$=\frac{4}{(n+1)^2}-\frac{6}{(n+1)^4}+\frac{4(n+1)^2}{(n+1)^6}-\frac{1}{(n+1)^6}$$

$$=\frac{4}{(n+1)^2}-\frac{6}{(n+1)^4}+\frac{4}{(n+1)^6}-\frac{1}{(n+1)^6}$$

Translating from $G_n$ to terms of $F_n$ generation:

$$\frac{4}{n^2}-\frac{6}{n^4}+\frac{4}{n^6}-\frac{1}{n^8}$$

### 4. *The polyhybrid*

We are now in a position to derive formulæ for solving the problem of the effect of eliminating all individuals who are not completely dominant from any polyhybrid strain. Let us repeat the formulæ just derived; which show the percentage of individuals who have some recessive characters in mono-, di-, tri-, and tetrahybrids;

Monohybrid $\frac{1}{n^2}$

Dihybrid $\frac{2}{n^2}-\frac{1}{n^4}$

Trihybrid $\frac{3}{n^2}-\frac{3}{n^4}+\frac{1}{n^6}$

Tetrahybrid $\frac{4}{n^2}-\frac{6}{n^4}+\frac{4}{n^6}-\frac{1}{n^8}$

The formulæ are all series of fractions with signs alternating plus and minus. The numerators in every case are given by all except the first term of the expanded binomial $-(1-1)^m$. The first term in each of the denominators is $n^2$ until the last term is reached which is $n^{2m}$.

Let $c_1, c_2, c_3, \cdots c_{m+1}$ be the successive terms of expanded binomial $(1+1)^m$. Then the formula for the elimination of all individuals not completely dominant from a polyhybrid stock would be:

$$\frac{c_2}{n^2}-\frac{c_3}{n^4}+\frac{c_4}{n^6}-\frac{c_5}{n^8}\cdots\pm\frac{1}{n^{2m}}$$

Or if we wish to express this in terms of $m!$:

$$\frac{m!}{1!m-1!n^2}-\frac{m!}{2!m-2!n^4}+\frac{m!}{3!m-3!n^6}-\cdots\pm\frac{m!}{m!0!n^{2m}}$$

As $n$ increases, the value of the latter terms of the formula so decrease in proportion to the first terms that they can be ignored without appreciably altering the value of the formula as a whole. Taking into consideration only the first two terms, the formula would read:

$$\frac{m}{n^2}-\frac{m(m+1)}{2n^4}$$

A further simplification would give the approximate formula:

$$\frac{m}{n^2}$$

which as $n$ increased would approach extremely close to the real value of the entire formula.

To illustrate: In an octahybrid stock the percentage of individuals who possessed some recessive trait in the $F_{20}$ generation is:

$$=\frac{8}{20^2}-\frac{28}{20^4}+\frac{56}{20^6}-\frac{70}{20^8}+\frac{56}{20^{10}}-\frac{28}{20^{12}}+\frac{8}{20^{14}}-\frac{1}{20^{16}}$$

$$=1.9825 \text{ percent}$$

Or, if we use only the first term:

$$2 \text{ percent}$$

## PART III

### THE ELIMINATION IN EACH GENERATION OF ALL INDIVIDUALS RECESSIVE FOR ALL $m$ INDEPENDENT FACTORS IN A POLYHYBRID OF $m$ ALLELOMORPHS

1. *Method of deriving zygotes of generation* $F_n$ *from gametes of generation* $G_n$

The problem presented in this section is attacked in the same manner as those in Parts I and II. In only the simplest case, that of eliminating the recessives from a monohybrid, (solved by JENNINGS (1916) whose equation, $1/(n+2)^2$, is modified to $1/n^2$ by changing the value of $n$ from the number of selections to the number of the filial generation $(F_n)$[1] has a formula been derived for expressing the effects of this type of selection in terms of $n$. The formulas for the polyhybrids are for calculating the gametes of generation $G_{n+1}$ in terms of generation $G_n$ and for determining the proportion of completely recessive individuals from any set of gametes. The method of deriving these formula is the same as that used in Part I.

If we group together all gametes which have the same number of dominant factors we will have $m+1$ such groups and, if the groups are arranged in order according to the number of dominant factors they contain beginning with the one which has all $m$ dominant factors and ending with one which is completely recessive, the number of different gametes in each successive group will be equal to the successive terms of the expanded binomial $(1+1)^m$. The zygotes of any generation $F_n$ are obtained by crossing the gametes of $G_n$ in all possible ways. This is best accomplished by squaring their sum. The completely recessive zygotes are produced only by a combination of gametes neither of which contains any dominant factors. According to our system of mating these homozygous recessive zygotes are obtained by squaring the completely recessive gametes. To obtain then the percentage of completely recessive individuals in the general population it is only necessary to divide the square of the completely recessive gamete by the square of the sum of all of the gametes which go to make up the population in question. Using the symbols $p$, $q$, $r$, $s$, etc., as in Parts I and II, we get the proportion of completely recessive individuals in the generation $F_n$ in terms of the gametes of $G_n$ expressed by the following formulæ:

$$\text{for the monohybrid} = \frac{q^2}{(p+q)^2}$$

[1] This formula, which forms the starting point for the series here treated, is the same one which formed the starting point for the series dealt with in Part II, for in the monohybrid these two schemes of selection would eliminate the same individual.

$$\text{for the dihybrid} = \frac{r^2}{(p+2q+r)^2}$$

$$\text{for the trihybrid} = \frac{s^2}{(p+3q+3r+s)^2}$$

$$\text{for the tetrahybrid} = \frac{t^2}{(p+4q+6r+4s+t)^2}$$

and so on.

### 2. *Method of deriving gametes of generation n+1 from gametes of generation* $G_n$

To obtain the gametes in generation $G_{n+1}$ in terms of those of $G_n$ we will proceed as in Part I and treat the gametes first as if they were immutable, that is, as if a zygote could produce only the gametes out of which it itself was formed. To repeat, this assumption is true when the zygote is homozygous or heterozygous for a single factor; it is not the case when the zygote is heterozygous for two or more factors.

Now the relative number of any gamete in generation $G_{n+1}$ can be easily calculated if the number of zygotes in generation $F_n$, which produce it, is known. According to our postulate, a gamete in generation $G_{n+1}$ would be produced from those zygotes in generation $F_n$ into whose formation went that same gamete in generation $G_n$. The number of these zygotes would be equal to the product of the gamete in question times the sum of the gametes. Thus in the case of the hybrid:

$$p_{n+1} = p_n(p_n+2q_n+r_n)$$

in the trihybrid:

$$p_{n+1} = p_n(p_n+3q+3r_n+s_n)$$

in the tetrahybrid:

$$p_{n+1} = p_n(p_n+4q_n+6r_n+4s_n+t_n)$$

Our scheme of selection eliminates but a single combination of gametes, $r^2$ in the dihybrid, $s^2$ in the trihybrid, $t^2$ in the tetrahybrid, etc. We can now write the complete formula, using the tetrahybrid as an example.

TABLE 33

$$\begin{aligned}
p_{n+1} &= p_n\,(p_n+4q_n+6r_n+4s_n+t_n)\\
q_{n+1} &= q_n\,(p_n+4q_n+6r_n+4s_n+t_n)\\
r_{n+1} &= r_n\,(p_n+4q_n+6r_n+4s_n+t_n)\\
s_{n+1} &= s_n\,(p_n+4q_n+6r_n+4s_n+t_n)\\
t_{n+1} &= t_n\,(p_n+4q_n+6r_n+4s_n)
\end{aligned}$$

It would be well to record here several interesting facts about the above formula. It would hold for all cases but for that "shifting" of gametes which occurs when the zygotes are heterozygous for two or more factors, which was discussed in Part I. This "shifting" does not occur at all in the monohybrid and in the polyhybrid does not affect any generation prior to $F_4$. This formula can consequently be used for the calculation of the gametes in any generation of the monohybrid and in generation $G_2$ and $G_3$ of the polyhybrid in terms of the gametes of the preceding generation. Combined with the formula for calculating the percentage of completely recessive individuals from any group of gametes, it can be stated in terms of $m$ and $n$. Thus:

$$\frac{1}{(n-2+2^m)^2}$$

It can be seen that the formula, $1/n^2$, for calculating the percentage of homozygous recessive individuals in the monohybrid when none are allowed to reproduce is but a special case of the above.

The "shifting" of gametes which occurs when the population is subjected to the type of selection we are now considering is essentially the same as that which occurs in Part I, and can best be described by a particular example. If we draw a diagonal line on table 33 from the upper right-hand corner at $p_n t_n$ to the lower left hand corner at $p_n t_n$ this line will cross all of the pairs which participate in a single shift, that is, $pt$, $qs$, $rr$, $sq$, and $tp$, lines drawn parallel with this diagonal from $p_n s_n$ and $q_n t_n$ respectively will each cross a group of the pairs which participate in another shift, that is, $ps$, $qr$ and $qt$, $rs$. Two more parallel lines from pair $p_n r_n$ and pair $t_n r_n$ will cross the pairs which participate in the remaining two "shifts," that is, $pr$, $qq$, and $rt$ $ss$. The number of times a particular combination of gametes participates within a shift is determined exactly the same as in Part I. It is necessary to give here only the results. Thus the effect of the single "shift" which occurs in the dihybrid is stated:

$$\frac{p_n r_n + q_n^2}{1}$$

In the trihybrid there are three shifts:

$$\frac{p_n r_n + q_n^2}{2},$$

$$\frac{p_n s_n + 3q_n r_n}{4} \text{ and } \frac{q_n s_n + r_n^2}{2}$$

In the tetrahybrid the shifts are:

$$\frac{p_n r_n + q_n^2}{2}, \quad \frac{p_n s_n + 3q_n r_n}{4}, \quad \frac{p_n t_n + 4q_n s_n + 3r_n^2}{8}, \quad \frac{q_n t_n + 3r_n s_n}{4}, \quad \frac{r_n t_n + s_n^2}{2}$$

In addition there is the single secondary shift $(q_n s_n + r^2_n)/2$.

These above stated "shifts" are substituted for gamete pairs exactly as in Part I though they have quite different coefficients. The following table, homologous to table 26, Part I, gives the coefficients of the primary "shifts" as they occur in the tetrahybrid.

TABLE 34

| $G_{n+1}$ | $G_n$ | $p$ | $q$ | $r$ | $s$ | $t$ |
|---|---|---|---|---|---|---|
| $p_{n+1}$ | $= p_n$ | ( 1 | + 4 | + 6 | + 4 | + 1) |
| $4q_{n+1}$ | $= 4q_n$ | ( 1 | + 3 | + 3 | + 1 | + 1) |
| $6r_{n+1}$ | $= 6r_n$ | ( 1 | + 2 | + 1 | + 2 | + 1) |
| $4s_{n+1}$ | $= 4s_n$ | ( 1 | + 1 | + 3 | + 3 | + 1) |
| $t_{n+1}$ | $= t^n$ | ( 1 | + 4 | + 6 | + 4) | |

The coefficients in the above table can be expressed in a general form which will hold for all polyhybrids. Let $d$ equal the number of dominant factors and $r$ the number of recessive which the gamete has whose value in generation $G_{n+1}$ is to be obtained. Then the coefficients of the shifts which are to replace the combinations in table 33 are the successive terms of the expanded binomial $(1+1)^d$ plus all except the first term of the expanded $(1+1)^r$. The combination $t_n^2$ is of course eliminated. By combining table 33 and 34 as the two like tables were combined in Part I, we can get the complete formulæ for obtaining gametes of generation $G_{n+1}$ in terms of $G_n$. The secondary shift which appears in the tetrahybrid is treated exactly as it is in Part I. The formulæ for obtaining $G_{n+1}$ from $G_n$ in the dihybrid and trihybrid:

*Dihybrid*

$$p_{n+1} = p_n^2 + 2p_n q_n + \frac{p_n r_n + q^2_n}{2}$$

$$q_{n+1} = p_n q_n + \frac{p_n r_n + q_n^2}{2} + q_n^2 + q_n r_n$$

$$r_{n+1} = \frac{p_n r_n + q_n^2}{2} + 2q_n r_n$$

*Trihybrid*

$$p_{n+1} = p_n^2 + 3p_n q_n + 3\frac{p_n r_n + q_n^2}{2} + \frac{p_n s_n + 3q_n r_n}{4}$$

$$q_{n+1} = p_n q_n + q_n^2 + 2\frac{p_n r_n + q_n^2}{2} + 2q_n r_n + \frac{p_n s_n + 3q_n r_n}{4} + \frac{q_n s_n + r_n^2}{2}$$

$$r_{n+1}=\frac{p_nr_n+q_n^2}{2}+2q_nr_n+\frac{p_ns_n+3q_nr_n}{4}+r_n^2+2\frac{q_ns_n+r_n^2}{2}+r_ns_n$$

$$s_{n+1}=\frac{p_ns_n+3q_nr_n}{4}+3\frac{q_ns_n+r_n^2}{2}+3r_ns_n$$

It would, of course, be desirable to obtain a formula which would allow us to calculate the percentage of completely recessive individuals appearing in any generation, $F_n$, without obtaining it for all preceding generations, under conditions in which none such are allowed to reproduce. Such a formula of course exists in the case of the monohybrid. No such exact formula has been derived for the polyhybrids. However it has been found that the percentage of such individuals which occur in those generations of the dihybrid which have been accurately worked out, when $n>7$, is very closely approximated by the formula:

$$\frac{\sqrt{n+?}-2.05}{n^2}$$

(see table 36.)

A formula in terms of $n$ which crudely shows the effects of selection upon the trihybrid is:

$$\frac{4}{(\sqrt{8n-15}+15)^2}$$

## PART IV.

### THE ELIMINATION IN EACH GENERATION OF ALL INDIVIDUALS (A) CONTAINING TWO OR MORE INDEPENDENT DOMINANT FACTORS, AND (B) CONTAINING THREE OR MORE INDEPENDENT DOMINANT FACTORS IN A POLYHYBRID OF $m$ ALLELOMORPHS

The problems in Parts I to III dealt with the results either of eliminating a certain completely defined combination or of retaining a certain completely defined combination. To illustrate with the pentahybrid:

Part I eliminates only the combination *ABCDE*

Part II retains only the combination *ABCDE*

Part III eliminates only the combination *aabbccddee*. (Retention of only this last combination, of course, leaves the stock at once uniformly pure recessive.)

The present Part IV deals with a case differing from those of the past three parts, in that any one of several combinations is eliminated and any one of several combinations is retained. Thus, when all individuals

containing any two or more dominants are eliminated, there are retained (1) all pure recessives, and (2) all that are dominant only in any one character. It appears desirable to deal briefly with these cases, as steps toward a general solution of the problem of eliminating individuals of any description from a polyhybrid.

It is quite possible that special ability in the human stock is determined by some such combination as we are now eliminating. It is obvious that all ability is not alike and consequently not determined by the same combination of genes though it may well be that different types of ability have some genes in common.

The generalized problem is: *Results of eliminating from a hybrid of m allelomorphs all individuals possessing any k or more dominant characters. Only the cases where k is 2 and where k is 3 are dealt with in the present paper.*

The formulæ here derived are for calculating the value of each kind of gamete in terms of the gametes of the preceding generation and for obtaining any given set of gametes from the percentage of zygotes to be eliminated. The formulæ are derived exactly as are those used in Part I, and can be obtained from tables 1 and 3. We shall derive formulæ for these different values of $m$—when $m=2$, $m=3$, and $m=4$—and from these further derive a generalized formula for any value of $m$. As the method of deriving the three sets of formulæ has already been explained (Part I) we will here merely give the formulæ in question.

1. The formulæ for showing the results of eliminating from a dihybrid stock any combination of two dominant factors has been derived in Part I. It is repeated here as it is the first of the series. The gametes of generation $G_{n+1}$ in terms of the gametes of generation $G_n$ are:

$$q_{n+1}=q_n(q_n+r_n)$$
$$r_{n+1}=r_n(2q_n+r_n)$$

noting that in this and all other cases here discussed, in generation $G_1$ all gametes are equal to unity.

The percentage of zygotes containing 2 dominant factors in terms of any set of gametes is:

$$\frac{2q^2}{(2q+r)^2}$$

2. When we eliminate each generation from a trihybrid all individuals who possess 2 or more dominant factors, the gametes of generation $G_{n+1}$ in terms of the gametes of generation $G_n$ are:

$$q_{n+1}=q_n(q_n+r_n)$$
$$r_{n+1}=r_n(3q_n+r_n)$$

The formula for calculating the percentage of zygotes eliminated in each generation in terms of these gametes is:

$$\frac{6q^2}{(3q+r)^2}$$

3. When $m=4$ the corresponding equations are for the gametes:

$$q_{n+1}=q_n(q_n+r_n)$$
$$r_{n+1}=r_n(4q_n+r_n)$$

and for the zygotes eliminated:

$$\frac{12q^2}{(4q+r)^2}$$

*To restate the above equations in a generalized form where m may have any value:* When any combination of 2 or more dominant factors is eliminated from a polyhybrid stock, the value of the gametes of any generation in terms of the gametes of the preceding generation is:

$$q_{n+1}=q_n(q_n+r_n)$$
$$r_{n+1}=r_n(mq_n+r_n)$$

The formula for deriving the percentage of zygotes containing 2 or more dominant factors from the above gametes is:

$$\frac{m(m-1)q^2}{(mq+r)^2}$$

To illustrate: The formulæ for showing the effects of eliminating any combination of 2 or more dominants from an octahybrid are (substituting in the above) for the gametes:

$$q_{n+1}=q_n(q_n+r_n)$$
$$r_{n+1}=r_n(8q_n+r_n)$$

and for the zygotes:

$$\frac{56q^2}{(8q+r)^2}$$

The effects of the aforementioned type of selection on various polyhybrid stocks are shown in table 37. It will be seen from this table that the individuals containing any combination of 2 or more dominant factors are eliminated more rapidly from a stock as $m$ increases. Thus these individuals disappear more slowly in a dihybrid than in any other stock.

B. *Results of eliminating in each generation all of the individuals, in a polyhybrid stock, that possess 3 or more dominant factors:* This problem is in all essentials identical with the one handled in A. We assign here, just as we did in A, three specific values to $m$ ($m=3$, $m=4$, and $m=5$) and generalize our resulting formulæ into such terms that $m$ may have any value.

We derive the gametes of generation $G_{n+1}$ in terms of those of generation $G_n$ exactly as in Part I, and calculate the percentage of zygotes eliminated each generation in terms of any given set of gametes.

1. The first case, that of the trihybrid ($m=3$) has been solved in Part I. When we eliminate from a trihybrid in each generation all individuals who possess 3 or more dominant factors, the gametes of generation $G_{n+1}$ in terms of those of $G_n$ are:

$$q_{n+1}=q_n{}^2+2q_nr_n+\frac{q_ns_n+r_n{}^2}{2}$$

$$r_{n+1}=2q_nr_n+2\frac{q_ns_n+r_n{}^2}{2}+r_ns_n$$

$$s_{n+1}=3\frac{q_ns_n+r_n{}^2}{2}+3r_ns_n+s_n{}^2$$

The percentage of zygotes eliminated each generation, in terms of the above, is:

$$\frac{6q(q+r)}{(3q+3r+s)^2}$$

When $m=4$ (the tetrahybrid) the corresponding formulæ are for the gametes:

$$q_{n+1}=q_n{}^2+2q_nr_n+\frac{q_ns_n+r_n{}^2}{2}$$

$$r_{n+1}=3q_nr_n+3\frac{q_ns_n+r_n{}^2}{2}+r_n{}^2+r_ns_n$$

$$s_{n+1}=\frac{q_ns_n+r_n{}^2}{2}+4r_ns_n+s_n{}^2$$

and for the zygotes:

$$\frac{6q(5q+4r)}{(6q+4r+s)^2}$$

3. When $m=5$ (the pentahybrid) the corresponding formulæ are for the gametes:

$$q_{n+1}=q_n{}^2+2q_nr_n+\frac{q_ns_n+r_n{}^2}{2}$$

$$r_{n+1}=4q_nr_n+4\frac{q_ns_n+r_n{}^2}{2}+r_n{}^2+r_ns_n$$

$$s_{n+1}=10\frac{q_ns_n+r_n{}^2}{2}+5r_ns_n+s_n{}^2$$

and for the zygotes:

$$\frac{30q\quad(3q\quad 2r)}{(10q+5r+s)^2}$$

4. The above series of equations derived for 3 specific values of $m$ can be expressed in a general form. Let $c_1, c_2, c_3 \cdot \cdot \cdot \cdot c_{n+1}$ be the successive terms of the expanded binomial $(1+1)^m$. Then, when any combination of three or more dominants is eliminated from a polyhybrid stock of $m$ allelomorphs, the gametes of generation $G_{n+1}$ in terms of the preceding generation $G_n$ are:

$$q_{n+1}=q_n{}^2+2q_nr_n+\frac{q_ns_n+r_n{}^2}{2}$$

$$r_{n+1}=(c_2-1)q_nr_n+(c_2-1)\frac{q_ns_n+r_n{}^2}{2}+r_ns_n$$

$$s_{n+1}=c_3\frac{q_ns_n+r_n{}^2}{2}+c_2r_ns_n+s_n{}^2$$

The percentage of zygotes eliminated in each generation in terms of these gametes is:

$$\frac{q\{[c_3(c_3-1)q+2[c_2c_3-c_2(c_2-1)]\}r}{(c_3q+c_2r+s)^2}$$

Illustrating with an octahybrid: If we let $m=8$, the corresponding formulæ are for the gametes:

$$q_{n+1}=q_n{}^2+2q_nr_n+\frac{q_ns_n+r_n{}^2}{2}$$

$$r_{n+1}=7q_nr_n+r_n{}^2+7\frac{q_ns_n+r_n{}^2}{2}+r_ns_n$$

$$s_{n+1}=28\frac{q_ns_n+r_n{}^2}{2}+8r_ns_n+s_n{}^2$$

and for the zygotes derived from them:

$$\frac{84q(9q+4r)}{(28q+8r+s)^2}$$

## GENERAL SUMMARY

It is obvious that before any of the results here obtained can be applied to a human population many more factors which enter into the problem of the effects of selection, must be evaluated. In every case here treated fortuitous mating was assumed, while in a human population it can scarcely be doubted that selective mating has a great influence upon the distribution and combination of those genes whose presence in an individual is a prerequisite for any special achievement. Linkage between certain of the genes concerned would also affect the results of selection—at least in the earlier generations. The present work has dealt with only certain of those effects of selection where there was a complete elimination of a certain type while in a human population such a complete elimination of a type must be quite rare. The relationship, however, between the number of genes which determine a given type and the recurrence of that type in a population in which it does not reproduce itself is a most important one and an evaluation of it is necessary to any understanding of the effects of selection. In a certain specific case, whose description follows, this has been done.

When all individuals dominant for all $m$ factors in a polyhybrid of $m$ allelomorphs are eliminated in the $F_2$ generation and the remainder of the population bred at random, there is a sudden sharp drop in the percentage of such individuals who appear in the $F_3$ generation. The results of a continued elimination of such individuals when plotted form a smooth curve which approaches zero as the number of such selections becomes infinite (figure 1). The more factors involved in the type that is eliminated (the greater the value of $m$), the slower the type is eliminated by selection. As we arbitrarily start with a population completely heterozygous in the $F_1$ generation and begin the selection process with generation $F_2$, the greater the value of $m$ the fewer the individuals we have to eliminate at the start. Thus the curve showing the rate of their disappearance begins at a lower point. A consequence of this and the slower disappearance of types determined by many genes is that each of these curves intersects all the others. A single selection ($F_3$) will bring the percentage of completely dominant individuals in a dihybrid stock below that of like individuals in a trihybrid and two selections ($F_4$) below those in a tetra-

hybrid. The trihybrid curve falls below that of the tetrahybrid in generation $F_7$. The ratios of the rates of disappearance of the completely dominant individuals in the various polyhybrid stocks are somewhat greater than the inverse ratios of the number of factors involved. Thus at the $F_{20}$ generation the percentage of completely dominant individuals in the dihybrid is less than two-thirds of those in the trihybrid which in turn is less than three-fourths of those in the tetrahybrid (table 35).

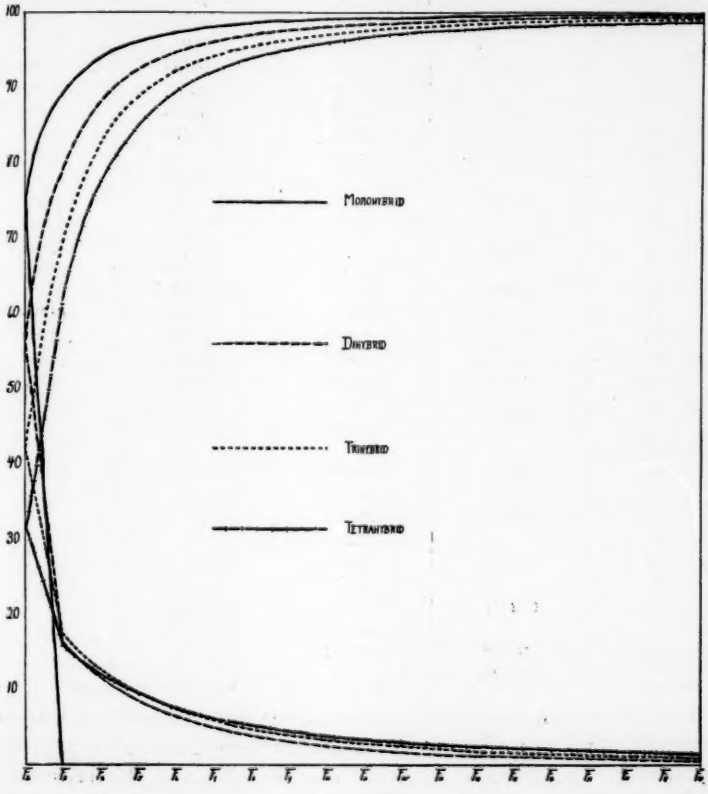


FIGURE 1.—The straight lines show the percentage of individuals dominant for all $m$ factors in a mono-, di-, tri-, and tetrahybrid when there is no selection. The upper curves show the percentage of such individuals appearing each generation when they alone are allowed to breed. The lower curves show the percentage of such individuals appearing in the stock when they are not allowed to breed and the rest of the stock bred at random.

TABLE 35

*Tables showing precentage of completely dominant individuals appearing each generation in several polyhybrid stocks, under conditions in which no completely dominant individual is allowed to breed.*

| | $\frac{2}{(n-\sqrt{\frac{n}{2}}+1)^2}$ | DIHYBRID | TRIHYBRID | TETRAHYBRID |
|---|---|---|---|---|
| $F_2$ | .500000 | .5625 | .4219 | .3164 |
| 3 | | .1632 | .1753 | .1578 |
| 4 | .1555 | .1189 | .1282 | .1217 |
| 5 | | .0876 | .0983 | .09460 |
| 6 | .0720 | .0658 | .07658 | .07590 |
| 7 | | .0505 | .06153 | .06248 |
| 8 | .0408 | .0397 | .04924 | .05236 |
| 9 | | .0309 | .04176 | .04453 |
| 10 | .0260 | .0260 | .03523 | .03836 |
| 11 | | .0215 | .03010 | .03341 |
| 12 | .01796 | .01807 | .02602 | .02936 |
| 13 | | .01534 | .02272 | .02603 |
| 14 | .01310 | .01317 | .01902 | .02326 |
| 15 | | .01128 | .01673 | .02090 |
| 16 | .00995 | .00999 | .01497 | .01890 |
| 17 | | .00880 | .01348 | .01719 |
| 18 | .00781 | .00781 | .01135 | .01569 |
| 19 | | .00693 | .01114 | .01440 |
| 20 | .00628 | .00626 | .01021 | .01327 |
| 21 | | .00566 | | |
| 22 | .00516 | .00512 | | |
| 23 | | .00467 | | |
| 24 | .00431 | .00427 | | |
| 25 | | .00391 | | |
| 26 | .00365 | .00360 | | |
| 27 | | .003325 | | |
| 28 | .003134 | .003078 | | |
| 29 | | .002869 | | |
| 30 | .002717 | .002663 | | |
| 31 | | .002485 | | |
| 32 | .002378 | .002325 | | |
| 100 | .000226 | | | |

Accurate formulæ were derived for calculating the percentage eliminated each generation in terms of the gametes produced by the preceding generation. The formulæ for describing the effects of this selection in terms of $n$ the number of the filial generation are more or less crude approximations which may be useful for extending the curves somewhat beyond the point where they have been accurately derived.

When the type of selection complementary to the above takes place, that is, when all individuals in a polyhybrid stock, that show any recessive

traits whatever, are eliminated, the effects can be stated much more simply, as the problem of these effects has been solved for all cases. The percentage of individuals to be eliminated each generation when plotted form a smooth curve, beginning with a value of $\frac{3}{4}^m$ in the $F_2$ generation and approximating zero at infinity (figure 1). As $n$ becomes large the percentage eliminated each generation is in direct proportion to the number of factors involved ($m$) and in inverse proportion to the square of the number ($n$) of the filial generation $F_n$. These effects can be expressed as $m/n^2$. The type here eliminated disappears somewhat more rapidly than its complementary type.

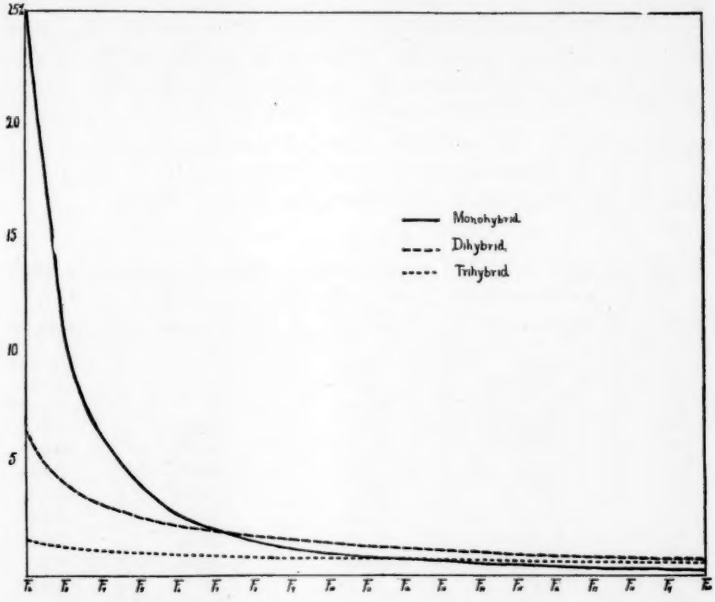


FIGURE 2.—Percentage of homozygous recessive individuals appearing each generation in a mono-, di-, and trihybrid stock when none such are allowed to breed and the rest of the stock bred at random.

When all individuals recessive for all $m$ factors in a polyhybrid of $m$ allelomorphs are eliminated the percentages of such individuals which appear in the various generations form, when plotted, curves of the same general shape as those just discussed. The percentage of homozygous recessives which appears in the $F_2$ generation is always $1/4^m$, thus as $m$

increases the curves start at much lower points (figure 2). The effects of the first selection (that which affects generation $F_3$) cause the completely recessive individual to disappear at the same rate regardless of the value of $m$. Thus the points $F_2$ and $F_3$ on the dihybrid curve occur on the monohybrid curve only further along (at $F_4$ and $F_5$) and the points $F_2$ and $F_3$ on the trihybrid curve occur at points still further along on the monohybrid (at $F_8$ and $F_9$). In the $F_4$ and subsequent generations of the polyhybrids the effects of "shifting" of gametes make themselves felt with the result that the eliminated type disappears much more slowly as $m$ increases. Thus although in the $F_2$ generation the percentage of completely recessive individuals was 25 in the monohybrid and but 6.25 in the dihybrid, in generation $F_7$ they were approximately the same in the two (2.04 and 1.96 respectively), while in the $F_{20}$ generation the percentage in the dihybrid was .66 to .25 in the monohybrid (table 36). Although the trihybrid curve has but a value of 1.56 in the $F_2$ generation it equals that of the monohybrid in generation $F_{12}$ and subsequently to this its value decreases so much less rapidly than the mono- and dihybrids that at about generation $F_{27}$ it crosses the dihybrid curve.

TABLE 36

*Tables showing the percentage of completely recessive individuals, appearing each generation under conditions in which no such individual is allowed to breed.*

| GENERATION | MONOHYBRID $(1/n^2)$ | DIHYBRID | $(n+2-2.05)/n^2$ | TRIHYBRID |
|---|---|---|---|---|
| $F_2$ | .25000 | .06250 | | .01562 |
| $F_3$ | .11111 | .04000 | | .01234 |
| $F_4$ | .06250 | .03095 | | .01093 |
| $F_5$ | .04000 | .02564 | .02380 | .01006 |
| $F_6$ | .02777 | .02222 | .02161 | .00939 |
| $F_7$ | .02040 | .01957 | .01938 | .00883 |
| $F_8$ | .01562 | .01744 | .01737 | .00833 |
| $F_9$ | .01234 | .01566 | .01564 | .00789 |
| $F_{10}$ | .01000 | .01417 | .01414 | .00748 |
| $F_{11}$ | .00826 | .01288 | .01286 | .00711 |
| $F_{12}$ | .00694 | .01180 | .01175 | .00677 |
| $F_{13}$ | .00591 | .01082 | .01078 | |
| $F_{14}$ | .00510 | .00998 | .00994 | |
| $F_{15}$ | .00444 | .00925 | .00921 | |
| $F_{16}$ | .00390 | .00859 | .00856 | |
| $F_{17}$ | .00346 | .00801 | .00799 | |
| $F_{18}$ | .00308 | .00748 | .00747 | |
| $F_{19}$ | .00277 | .00702 | .00701 | |
| $F_{20}$ | .00250 | .00660 | .00660 | |
| $F_{100}$ | .00010 | | .00080 | .00216 |

A comparison of the results obtained by eliminating completely recessive individuals and by eliminating completely dominant individuals would

indicate that, when the number of genes is the same in both cases, the recessive is eliminated much more slowly than the dominant. Thus in the $F_2$ generation of the dihybrid the percentage of individuals dominant for $m$ factors is $56\frac{1}{4}$ while the percentage recessive for $m$ factors is but $6\frac{1}{4}$, in generation $F_{20}$ the percentage of completely dominant individuals has been reduced to .626 which is less than the percentage of complete recessives in this generation (.66). In generation $F_{100}$ their values would be .023 and .081 respectively. In generation $F_{100}$ of the trihybrid the complete recessive would also occur about four times as frequently as the complete dominant.

These results are in keeping with the findings of WARREN when he investigated the effects of selection upon a monohybrid stock under conditions approximating those found in nature. He found that the elimination of the less viable type was more rapid when it was of a dominant form.

When any combination of two or more dominants is eliminated from a polyhybrid of $m$ allelomorphs in the $F_2$ and subsequent generations, it continues to appear in decreasing numbers. The greater the value of $m$, the greater the percentage of such combinations which appear in the $F_2$ generation and the more rapidly is the type eliminated (table 37).

TABLE 37

*The percentage of individuals eliminated (all of those who have 2 or more dominant factors) in each generation from:*

| GENERATION | DIHYBRID | TRIHYBRID | TETRAHYBRID | OCTAHYBRID |
|---|---|---|---|---|
| $F_2$ | .5625 | .84375 | .94922 | .99952 |
| $F_3$ | .1632 | .24000 | .28402 | .35840 |
| $F_4$ | .1189 | .14958 | .16064 | .16856 |
| $F_5$ | .0876 | .09683 | .09729 | .09150 |
| $F_6$ | .0658 | .06557 | .06355 | .05700 |
| $F_7$ | .0505 | .04698 | .04428 | .03866 |
| $F_8$ | .0397 | .03504 | .03242 | .02786 |
| $F_9$ | .0309 | .02700 | .02467 | .02100 |
| $F_{10}$ | .0260 | .02138 | .01936 | .01637 |

Consequently when the percentage of the type is plotted against the filial generations, the curves of the various polyhybrids intersect as shown in figure 3.

## *Summary of formulæ*

In the formulæ the symbols used have the following values: $n$ = the number of the filial generation $F_n$, $m$ = the number of genes concerned; $c_1, c_2, c_3, c_4 \cdots c_{n+1}$ = the successive terms of the expanded binomial

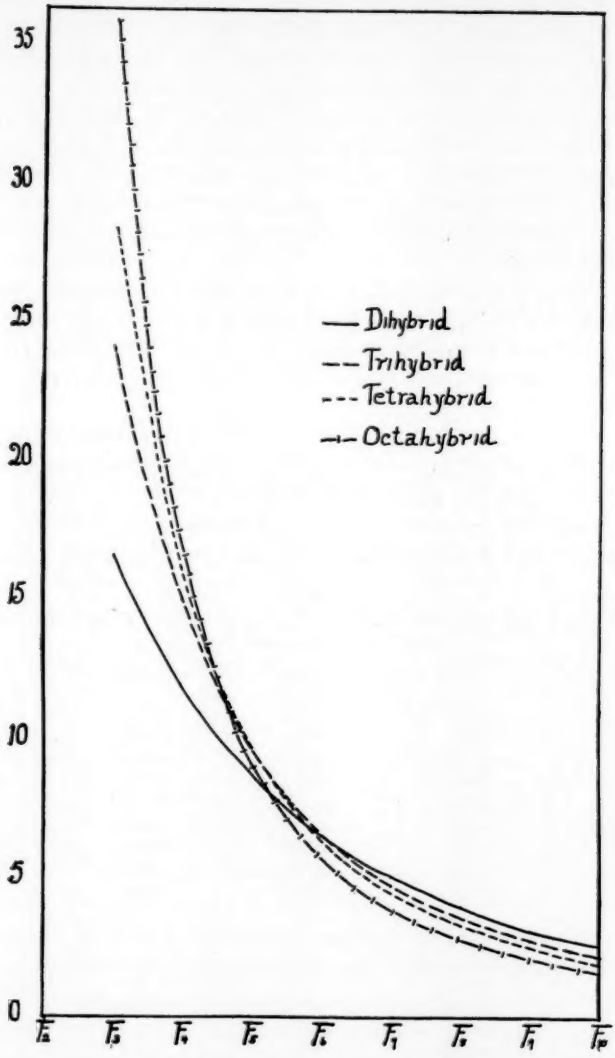


FIGURE 3.—Percentage of individuals containing two or more dominant factors in a di-, tri-, tetra- and octahybrid stock when none such are allowed to breed.

$(1+1)^m$; $p$ = the group of gametes having all $m$ dominant factors; $q$ = the group having $m-1$ dominant factors; $r$ = the group having $m-2$ and so on. In all instances the stock is completely heterozygous in the $F_1$ generation and selection starts in generation $F_2$.

I. Formulæ for calculating the percentage of completely dominant individuals appearing in a stock where none such are allowed to breed.

1. In the case of the dihybrid: Gametes of generation $G_{n+1}$ in terms of gametes of $G_n$ (In $G_1$ all gametes equal 1):

$$q_{n+1}=q_n(q_n+r_n)$$
$$r_{n+1}=r_n(2q_n+r_n)$$

The percentage of zygotes containing all $m$ dominant factors in terms of any given set of gametes:

$$\frac{2q^2}{(2q+r)^2}$$

An approximate formula which gives very nearly the true values expressing the percentage in terms of $n$, when $n>7$:

$$\frac{2}{\left(n-\sqrt{\frac{n}{2}}+1\right)^2}$$

2. In the case of the trihybrid. The gametes are:

$$q_{n+1}=q_n{}^2+2q_nr_n+\frac{q_ns_n+r_n{}^2}{2}$$

$$r_{n+1}=2q_nr_n+r_n{}^2+2\frac{q_ns_n+r_n{}^2}{2}+r_ns_n$$

$$s_{n+1}=3\frac{q_ns_n+r_n{}^2}{2}+3r_ns_n+s_n{}^2$$

The percentage of zygotes containing all $m$ factors in terms of the gametes:

$$\frac{6q(q+r)}{(3q+3r+s)^2}$$

A formula expressing the percentage in terms of $n$ which is fairly accurate when $n>7$:

$$=\frac{2+\frac{\log(n-3)}{\log 4}}{n^2}$$

3. In the case of the tetrahybrid, the gametes are:

$$q_{n+1}=q_n{}^2+3q_nr_n+3\frac{q_ns_n+r_n{}^2}{2}+\frac{q_nt_n+3r_ns_n}{4}$$

$$r_{n+1}=2q_nr_n+4\frac{q_ns_n+r_n{}^2}{2}+r_n{}^2+2\frac{qnt_n+3r_ns_n}{4}+2_ns_n+\frac{r_nt_n+s_n{}^2}{2}$$

$$s_{n+1}=\frac{3q_ns_n+r_n{}^2}{2}+3\frac{q_nt_n+3r_ns_n}{4}+3r_ns_n+3\frac{r_nt_n+s_n{}^2}{2}+s_n{}^2+s_nt_n$$

$$t_{n+1}=4\frac{q_nt_n+3r_ns_n}{4}+6\frac{r_nt_n+s_n{}^2}{2}+4s_nt_n+t_n{}^2$$

The percentage of zygotes containing all $m$ factors in terms of the gametes:

$$\frac{4q(3q+6r+2s)+6r^2}{(4q+6r+4s+t)^2}$$

A crudely approximate formula for expressing this percentage in terms of $n$, when $n>7$:

$$\frac{1+\dfrac{\log\,(n-3)}{\log\quad 2}}{n^2}$$

Methods for deriving formulæ for other polyhybrids where $m>4$ are given in PART I.

II. Formulæ for calculating the percentage of individuals who show some successive character in a stock where only completely dominant individuals are allowed to breed.

1. In the case of the monohybrid:

$$\frac{1}{n^2}$$

2. In the case of the dihybrid:

$$\frac{2}{n^2}-\frac{1}{n^4}$$

3. In the case of the trihybrid:

$$\frac{3}{n^2}-\frac{3}{n^4}+\frac{1}{n^6}$$

4. In the case of the tetrahybrid:

$$\frac{4}{n^2}-\frac{6}{n^4}+\frac{4}{n^6}-\frac{1}{n^8}$$

5. In the case of the polyhybrid:

$$\frac{c_2}{n^2}-\frac{c_3}{n^4}+\frac{c_4}{n^6}-\frac{c_5}{n^8}\cdots\frac{1}{n^{2m}}$$

Expressed in terms of $m$:

$$\frac{m!}{1!m-1!n^2}-\frac{m!}{2!m-2!}+\frac{m!}{3!m-3!n^6}\cdots\pm\frac{m!}{m!0!n^{2m}}$$

Ignoring the latter term of the formula, whose value soon becomes negligible, and using only the first two terms:

$$\frac{m}{n^2}-\frac{m(m-1)}{2n^4}$$

As $n$ increases the first term soon approximates the value of the entire formula:

$$\frac{m}{n^2}$$

III. Formulæ for calculating the percentage of completely recessive individuals in a stock where none such are allowed to breed.

1. For the monohybrid:

$$\frac{1}{n^2}$$

2. For the $F_2$ and $F_3$ generations of any polyhybrid:

$$\frac{1}{(n-2+2^m)^2}$$

3. In the case of the dihybrid the gametes are:

$$p_{n+1}=p_n{}^2+2p_nq_n+\frac{p_nr_n+q_n{}^2}{2}$$

$$q_{n+1}=p_nq_n+q_n{}^2+\frac{p_nr_n+q_n{}^2}{2}+q_nr_n$$

$$r_{n+1}=\frac{p_nr_n+q_n{}^2}{2}+2q_nr_n$$

The percentage of zygotes, homozygous recessive for all $m$ factors:

$$\frac{r^2}{(p+2q+r)^2}$$

An approximate formula whose value is extremely close to the true value determined by the above when $n>7$:

$$\frac{\sqrt{n+2}-2.05}{n^2}$$

4. In the case of the trihybrid, the gametes are:

$$p_{n+1}=p_n^2+3p_nq_n+3\frac{p_nr_n+q_n^2}{2}+\frac{p_ns_n+3q_nr_n}{4}$$

$$q_{n+1}=p_nq_n+q_n^2+2\frac{p_nr_n+q_n^2}{4}+2q_nr_n+\frac{p_ns_n+3q_nr_n}{4}+\frac{q_ns_n+r_n^2}{2}$$

$$r_{n+1}=\frac{p_nr_n+q_n^2}{4}+2q_nr_n+\frac{p_ns_n+3q_nr_n}{2}+r_n^2+2\frac{q_ns_n+r_n^2}{2}+r_ns_n$$

$$s_{n+1}=\frac{p_ns_n+3q_nr_n}{4}+3\frac{q_ns_n+r_n^2}{2}+3r_ns_n$$

The percentage of zygotes, homozygous recessive for all $m$ factors:

$$\frac{s^2}{(p+3q+3r+s)^2}$$

A formula which crudely approximates the above:

$$\frac{4}{(\sqrt{8n-15}+15)^2}$$

Methods for deriving formulæ for other polyhybrids are given in PART III.

IV. 1. Formulæ for expressing the percentage of individuals containing 2 or more dominant factors in a polyhybrid of $m$ allelomorphs when none such are allowed to breed.

The gametes are:

$$q_{n+1}=q_n(q_n+r_n)$$
$$r_{n+1}=r_n(mq_n+r_n)$$

The percentage of zygotes to be eliminated in terms of any given set of gametes is:

$$\frac{m(m-1)q^2}{(mq+r)^2}$$

2. Formula for expressing the percentage of individuals containing 3 or more dominant factors in a polyhybrid of $m$ allelomorphs when none such are allowed to breed:

The gametes are:

$$q_{n+1}=q_n^2+2q_nr_n+\frac{q_ns_n+r_n^2}{2}$$

$$r_{n+1}=(c_2-1)q_nr_n+(c_2-1)\frac{q_ns_n+r_n^2}{2}+r_n^2+r_ns_n$$

$$s_{n+1}=c_3\frac{q_ns_n+r_n^2}{2}+c_2r_ns_n+s_n^2$$

The percentage of zygotes to be eliminated is:

$$\frac{q\left\{[(c_3c_3-1)q+2[c_2c_3-c_2+(c_{2-1})]r\right\}}{(c_3q+c_2r+s)^2}$$

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# EFFECTS OF TEMPERATURE ON LENGTH OF VESTIGIAL WING IN *DROSOPHILA VIRILIS*[1]

J. ERNEST NADLER

*Zoological Laboratory, The Johns Hopkins University, Baltimore, Maryland*

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TABLE OF CONTENTS

| | PAGE |
|---|---|
| INTRODUCTION | 584 |
| Material and methods | 585 |
| Experimental data | 586 |
| SUMMARY | 588 |
| LITERATURE CITED | 589 |

## INTRODUCTION

While carrying on selection experiments with the vestigial wing form of *Drosophila ampelophila*, ROBERTS (1918) noted that during the summer months the length of the wing increased. He later placed some of the progeny in an incubator at about 28 degrees and the rest at room temperature of about 22 degrees. He concluded that the length of the vestigial wing increases with an increase in the temperature and that the males are affected more by high temperature than are the females.

The present paper records an attempt to ascertain whether low as well as high temperatures modify the wing length of Drosophila, and whether the change resembles that of a chemical reaction. It has been found in the case of homogeneous reactions that a rise of 10 degrees in the temperature increases the rate of reaction 2 to 4 times, or, on the average, by 2.5 times. This applies to all reactions, whether they take place under the influence of a catalyst or not. The rate of increase falls, to a greater or less extent, as the temperature rises. When one considers not single reactions but the complex life processes as a whole, it is found that in these cases also a similar relationship exists between temperature and rate of reaction so that a rise of 10 degrees in the temperature is accompanied by a doubling or a trebling of the rate at which life processes take place. This has been shown by WOODRUFF and BAITSELL (1911) with *Paramaecium aurelia* and LOEB and NORTHROP (1917) with Drosophila. They demonstrated that life is lived more rapidly at a temperature higher than normal.

[1] I am indebted to Professor H. S. JENNINGS and Doctor ALEXANDER WEINSTEIN for suggestions in connection with this work.

## MATERIAL AND METHODS

The offspring of the mating of a single pair of a vestigial stock of *Drosophila virilis* furnished by Doctor ALEXANDER WEINSTEIN were used as a basis of all the experiments. As a number of preliminary experiments were made during the winter of 1924–1925, these individuals were bred together for a whole year before the experiments recorded below were carried out. To insure virginity, the females were picked out of the breeding bottles within 3 hours after hatching. The matings were made with a single male and female in a breeding bottle. Individuals of nearly similar body size and wing length were mated in an attempt to make all conditions as nearly equal as possible. After they had been in the breeding bottle some time the pair were transferred to a second bottle and then to a third so as to secure eggs in three bottles. No attempt was made to count the number of eggs laid in each bottle, but the presence of eggs in each bottle was ascertained. One bottle was then placed at a low temperature (usually 12 degrees, maximum range 9 to 13 degrees), another at room temperature (18 to 22 degrees) and the third at a high temperature (29 to 30 degrees).

Many eggs placed at the low temperature failed to develop to maturity. It was difficult to determine whether this was due to a reduction in their vitality with a decrease in temperature or whether other factors in the environment such as bacterial changes in the banana agar, or mold, killed them. For the purpose of this comparative study only those families which produced progeny at all temperatures were used.

The offspring were preserved in 75 percent alcohol for three weeks before the measurements were made. The longitudinal vein III[2] of the right wing was measured in each case and this length used as a standard for comparison, and, in addition, the *tibia* of the right front leg was measured. In a few instances the distance between the eyes and the length of the thorax were also measured. These measurements were used as an index of the size of the individual. Measurements were made with the low power of a binocular microscope fitted with a measuring ocular in the right ocular. The ocular micrometer was calibrated against a Leitz stage micrometer.

The flies were fed in the usual manner with fermented banana, as described by MORGAN, STURTEVANT, MULLER and BRIDGES (1915). Some individuals were lost by sticking in the banana agar and a few had to be discarded owing to excessive curling of the wings, which prevented measuring.

[2]The terminology is after MORGAN, BRIDGES and STURTEVANT, 1925, p. 6.

## EXPERIMENTAL DATA

The results obtained may be illustrated by presenting a typical example (table 1) and a summary (table 2).

TABLE 1

*Wing lengths of individuals of sub-family A12, in units each of which is one mu.*

| P | $F_1$ | | |
|---|---|---|---|
| | 9°–13° | 18°–22° | 29°–30° |
| 24.67 | 9.67 | 25.93 | 24.61 |
| 24.64 | 11.8 | 23.8 | 27.5 |
| | 12.75 | 23.55 | 19.9 |
| | 8.55 | 23.75 | 33.82 |
| | 9.5 | 18.64 | 28.73 |
| | 8.83 | 20.15 | 20.95 |
| | 12.91 | 19.1 | 39.44 |
| | 7.24 | 22.37 | 29.35 |
| | 5.28 | 18.75 | |
| | 13.37 | 17.74 | |
| | 8.4 | 18.8 | |
| | 10.5 | 20.57 | |
| | 7.89 | 20.35 | |
| | 10.57 | | |
| | 10.32 | | |

We may now compare the effect of temperatures on wing length with their effects on the velocity of chemical reactions. Using the well known formula for the temperature coefficient,

$$Q_{10} = \left(\frac{K_1}{K_0}\right)\frac{10}{T_1 - T_0}$$

in which $Q_{10}$ is the coefficient of the rate of increase in the reaction for a rise of 10 degrees C and $K_1$ and $K_0$ represent constants observed at the temperatures $T_1$ and $T_0$ respectively, it is found that the mean $Q_{10}$ derived from the data presented in table 2 is 1.98 (see tables 3 and 4).

An analysis of tables 3 and 4 shows that the wing length of Drosophila is affected more by lowering the temperature below the usual condition than by raising the temperature. As already pointed out, this is to be expected on the basis of the effect on the speed of a chemical reaction. Although the $Q_{10}$ in every case is somewhat lower than that obtained for a simple chemical reaction, the temperature coefficients are in striking agreement with the demands of the *van't* HOFF law.

The body size of the progeny of both small and large flies varied greatly and there appeared to be no particular correlation between the size of

TABLE 2

*Average wing length of $F_1$ at different temperatures. (Unit equals one mu.)*

| CASE | $F_1$* WING LENGTH | 9°–13° NO. OF $F_1$ | ♂ | ♀ | Both | 18°–22° NO. OF $F_1$ | ♂ | ♀ | Both | 29°–30° NO. OF $F_1$ | ♂ | ♀ | Both |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| A12 | 24.67<br>24.64 | 15 | 11.12 | 8.37 | 9.83 | 13 | 21.68 | 20.48 | 21.03 | 8 | 27.28 | 28.82 | 28.03 |
| A40 | 20.20<br>19.96 | 9 | 9.69 | 12.78 | 11.29 | 20 | 17.51 | 18.20 | 17.99 | 6 | 35.10 | 30.16 | 30.98 |
| C3 | 22.80<br>22.75 | 11 | 11.41 | 10.63 | 10.96 | 7 | 16.81 | 22.05 | 19.94 | 11 | 26.64 | 27.97 | 27.60 |
| D25 | 20.36<br>20.00 | 11 | 8.55 | 8.00 | 8.25 | 13 | 19.15 | 21.21 | 20.43 | 12 | 29.82 | 31.64 | 30.41 |
| D31 | 24.78<br>25.16 | 3 | 10.83 | none | 10.83 | 13 | 22.62 | none | 22.62 | 4 | 28.95 | none | 28.95 |
| D32 | 17.45<br>17.30 | 5 | 11.12 | 14.20 | 11.73 | 14 | 18.13 | 22.53 | 20.50 | 4 | 36.19 | 28.00 | 30.05 |
| D37 | 22.00<br>21.93 | 5 | 10.71 | 10.83 | 10.76 | 13 | 22.10 | 21.14 | 21.51 | 8 | 36.67 | 35.29 | 36.23 |
| G2 | 23.50<br>23.60 | 4 | 10.69 | 11.36 | 10.70 | 5 | 21.35 | 20.02 | 20.82 | 8 | 33.68 | 31.38 | 32.53 |
| H5 | 19.70<br>19.70 | 2 | 12.41 | 9.73 | 11.07 | 8 | 22.88 | 21.52 | 22.22 | 5 | 39.32 | 35.83 | 37.35 |
| H20 | 19.38<br>19.43 | 7 | 9.63 | 12.79 | 11.44 | 6 | 21.55 | 23.37 | 22.46 | 9 | 37.05 | 33.95 | 35.67 |
| H22 | 15.45<br>15.50 | 7 | 10.94 | 8.69 | 9.66 | 10 | 19.39 | 22.26 | 20.54 | 11 | 35.73 | 32.61 | 33.12 |
| K7 | 18.56<br>18.62 | 2 | 12.25 | none | 12.25 | 16 | 21.97 | 21.19 | 20.36 | 8 | 31.02 | 29.14 | 29.61 |
| Total average | | | 10.77 | 10.73 | 10.73 | | 20.42 | 21.36 | 20.86 | | 33.12 | 31.34 | 31.71 |

*Reared at room temperature.

the body and the length of the wing. Some large flies had very short wings while many large individuals had long wings and *vice versa*. There was likewise no striking difference between the sexes.

The average length of time required for flies bred at 9 to 13 degrees to

reach the Imago stage was 90 days; those kept at 18 to 22 degrees, 15 days; those raised at 29 to 30 degrees, 8 days.

TABLE 3

*Temperature coefficient for temperatures below and above room temperature.*

| CASE | $Q_{10}$(12°–20°) | $Q_{10}$(20°–30°) |
|---|---|---|
| A 12 | 2.66 | 1.33 |
| A 40 | 1.98 | 1.72 |
| C 3 | 2.26 | 1.38 |
| D 25 | 3.1 | 1.48 |
| D 31 | 2.6 | 1.27 |
| D 32 | 2.17 | 1.46 |
| D 37 | 2.48 | 1.68 |
| G 2 | 2.41 | 1.56 |
| H 5 | 2.5 | 1.68 |
| H 20 | 2.45 | 1.58 |
| H 22 | 2.65 | 1.61 |
| K 7 | 2.07 | 1.4 |

TABLE 4

*Average temperature coefficient.*

| | |
|---|---|
| Average $Q_{10}$ of all cases 12°–20° | 2.44 |
| Average $Q_{10}$ of all cases 20°–30° | 1.51 |
| Average $Q_{10}$ for all temperatures | 1.98 |

The change in wing length due to temperature is not hereditary. $F_2$ from parents bred respectively at 12 degrees and at 30 degrees, when bred at 20 degrees had a wing length similar to those raised from parents at 20 degrees. In the case of $F_1$ raised at 30 degrees many individuals had apparently normal wings in respect to size and shape but were unable to fly.

## SUMMARY

1. The vestigial wing length of *Drosophila virilis* is modified by changes in temperature in the manner of a chemical reaction. The temperature coefficient ($Q_{10}$) is approximately 1.98.

2. Low temperatures affect this character more than high temperatures. The temperature coefficient for the range between 12 and 20 degrees is approximately 2. 44, while that between 20 and 30 degrees is 1.15.

3. The changes in wing length due to temperature are not hereditary, when the offspring are bred at room temperature.

4. There is thus need of maintaining a constant temperature during the study of the genetics of wing length of Drosophila.

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# CYTOLOGICAL AND GENETIC STUDIES ON FRAGARIA

K. ICHIJIMA

*Bussey Institution, Harvard University, Boston, Massachusetts*

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TABLE OF CONTENTS

| | PAGE |
|---|---|
| INTRODUCTION | 590 |
| Methods | 592 |
| Chromosome details | 592 |
| a. Chromosomes of the European type | 592 |
| b. Chromosomes of the Haut-bois type | 593 |
| c. Chromosomes of the American type | 593 |
| d. Chromosomes of the Chilean type | 593 |
| e. Chromosomes of the Cultivated-variety type | 593 |
| d. Chromosomes in $F_1$ hybrids and $F_2$ hybrids | 596 |
| DISCUSSION | 597 |
| a. Polyploidy in the Fragaria species | 597 |
| b. Species hybrids | 600 |
| SUMMARY | 601 |
| LITERATURE CITED | 602 |

## INTRODUCTION[1]

The eleven species and twelve cultivated varieties of the genus Fragaria which were included in this investigation may be divided into five different groups:

Group 1.—The European type, represented typically by the species *F. vesca* which is the most common wild species in Europe and is also widely distributed over NORTH AMERICA and western South America.

*Fragaria vesca* L.

*F. americana* Britton.

[1] Several genetic investigations on the genus Fragaria were started at the BUSSEY INSTITUTION in 1921 with material furnished by Mr. G. M. DARROW of the UNITED STATES DEPARTMENT OF AGRICULTURE. Mr. DARROW has very kindly visited the laboratory several times, has identified and checked the living material, and has made many suggestions of great value during the progress of the work.

In 1924, Mr. K. ICHIJIMA undertook to make a cytological examination of all of the pure species and of the most interesting hybrids then on hand. This study he finished in the spring of 1925, but was unable to make a detailed report at that time because of a long illness. In the winter of 1925–1926, however, the present paper was written, and left to the undersigned to edit.

In the meantime, a paper entitled "Chromosomes and their significance in strawberry classification," by Dr. A. E. LONGLEY, was published in the Journal of Agricultural Research 32: 559–568, issued March 15, 1926. The data reported here corroborate many of Dr. LONGLEY's results and furnish certain additional facts. Both papers gain in value from having been written simultaneously and independently. E. M. EAST

*F. californica* Cham. & Schlecht.
*F. mexicana* Schlecht.
*F. Helleri* Holz.
*F. bracteata* Heller.

Group 2.—The Haut-bois type, represented by *F. elatior*, indigenous to Europe.

*Fragaria elatior* Ehrh.

Group 3.—The American type, represented typically by the species *F. virginiana* which is very widely distributed in North America.

*Fragaria virginiana* Duchesne.
*F. glauca* Rydb.

Group 4.—The Chilean type, indigenous to the Pacific Coast of North and South America and represented by the species *F. chiloensis*.

*Fragaria chiloensis* Duchesne.
*F. cuneifolia* Nutt? from Oregon.

Group 5.—Certain cultivated varieties of a type often described as *F. grandiflora* in the Taxonomy of the genus.

Varieties used:

| | | |
|---|---|---|
| William Belt | La Pearl | Ettersburg |
| Champion Early | Clark's Seedling | Gardners |
| New York | Doctor Burrell | Progressive |
| | Chesapeake | Success |

In addition to the above, the following hybrids were examined:

$F_1$ hybrids between the species—

*F. vesca* ♀ × *F. Helleri* ♂
*F. vesca* ♀ × *F. americana* ♂
*F. Helleri* ♀ × *F. americana* ♂
*F. bracteata* ♀ × *F. Helleri* ♂ . . . . (type a)
*F. bracteata* ♀ × *F. Helleri* ♂ . . . . (type b)
*F. glauca* ♀ × *F. virginiana* ♂
*F. bracteata* ♀ × *F. virginiana* ♂
*F. mexicana* ♀ × *F. virginiana* ♂
*F. bracteata* ♀ × *F. glauca* ♂
*F. americana* ♀ × *F. glauca* ♂
*F. grandiflora* var. *Dunlap* ♀ × *F. platypetala* ♂

RYDBERG's (1912) descriptions have been followed in making up the above list. The species which he designates as *F. Helleri*, however, is merely a pink-flowered variety of *F. vesca*.

## METHODS

Maturation divisions occur very early in Fragaria flowers, and the chromosomes are very minute. For these reasons it was necessary to modify the cytological methods ordinarily in use in several particulars.

Flower buds were collected when about 1 mm in diameter, the calyx stripped off and fixed for 12 hours. For somatic chromosome counts, very young, thick root-tips from newly produced runners were found to be the most suitable material. As fixatives, Flemming's medium solution and chrom-acetic acid were found to be unsatisfactory. Bouin's solution as modified by ALLEN (1916) gave much better results, except in the hybrid between *F. bracteata* and *F. Helleri*, where straight Bouin's solution was used.

The material was washed 5 hours in water and then moved up through the alcohols. It was found necessary to transfer slowly to xylol, keeping the material 4 hours each in various percentages beginning with 15 percent.

The paraffine blocks cut very satisfactorily and the material examined unstained was not shrunken. But if care was not taken in staining, shrinkage was quite marked.

The best method of staining was found to be the use of 4 percent iron-alum as a mordant for only 2 hours, followed by transfer to haemotoxylin for 3 hours. No destaining was necessary.

## CHROMOSOME DETAILS

### a. *Chromosomes in Group 1—the European type*

All of the six species of this group which were investigated have 7 pairs of chromosomes in the pollen mother cells. No irregular behavior of the chromosomes in the course of the heterotypic division was observed. In the earliest stage the pollen mother cells are closely packed in the anther cavity. As the meiotic division proceeds the cells gradually begin to separate from one another. After the synapsis there is generally a distinct spireme stage in which the double thread-like nature can clearly be seen; but no second contraction has been observed. At early diakinesis the paired chromosomes are often unequal in size (figure 1), but gradually contract into a uniform size in the later stage. At this stage the 7 pairs of chromosomes can be seen clearly (figure 2). When the paired chromosomes become almost spherical the nucleolus and nuclear membrane disappear. The chromosomes then gather toward the center and arrange themselves on the equatorial plate. It is here at the metaphase and at the late anaphase that the chromosomes can be most readily counted (figures

3, 4). After the telophase and the subsequent resting stage the cells begin the homeotypic division which is carried out in the regular manner (figure 5), the resulting tetrads being quite normal. The 14 somatic chromosomes are seen clearly and may be counted readily at the metaphase of the root-tip cell (figure 6). The somatic chromosomes appear in a characteristic figure and are all separated from one another in well fixed preparations.

b. *Chromosomes in Group 2—The Haut-bois type*

In the single species, *F. elatior*, belonging to this group, the gametic number of chromosomes in the pollen mother cell is 21. Figure 7 shows the chromosomes in the heterotypic metaphase. There is no irregular behavior of the chromosomes during the whole process of maturation which indicates the stability of the species cytologically.

c. *Chromosomes in Group 3—The American type*

Two species of this type were investigated, *F. virginiana* and *F. glauca*. Both of them possess 28 chromosomes as the gametic number. Owing to the minute size of the pollen mother cell it is quite difficult to count the chromosomes when such large numbers are present. After a number of experiments it was found that counts could best be made in the late diakinesis of the heterotypic division (figure 8). The somatic chromosomes are closely and irregularly packed in the small root-tip cells. The somatic number of chromosomes could not be determined definitely although it appears to be approximately 56.

d. *Chromosomes in Group 4—The Chilean type*

*F. chiloensis* and *F. cuneifolia* both show 28 chromosomes as the gametic number. The behavior of the chromosomes is quite regular throughout both the heterotypic and the homeotypic divisions. No abnormalities in chromosomal behavior were found (figures 9, 10).

e. *Chromosomes in Group 5—The Cultivated variety type*

Twenty-eight pairs of chromosomes were in found the pollen mother cells of each of these varieties. Abundant pollen grains are produced and the process of reduction appears to be regular. There is little difference in the chromosome behavior between this type and the American type, both of which have the same number of the chromosomes (figure 11).

PLATE I

FIGURE 1.—The 7 paired chromosomes at diakinesis in *Fragaria vesca* var.

FIGURE 2.—A later stage of the same.

FIGURE 3.—Metaphase of heterotypic division.

FIGURE 4.—Late anaphase.

FIGURE 5.—Metaphase of homeotypic division.

FIGURE 6.—Metaphase of division in the root-tip cell (14 somatic chromosomes).

FIGURE 7.—Metaphase showing 21 pairs of chromosomes (*F. elatior*).

FIGURE 8.—Diakinesis showing 28 paired chromosomes (*F. virginiana*).

FIGURE 9.—The same stage in *F. chiloensis*.

FIGURE 10.—Homeotypic metaphase of the same.

FIGURE 11.—Diakinesis showing 28 paired chromosomes (a cultivated variety).

FIGURE 12.—Metaphase of the $F_1$ hybrid of *F. bracteata*×*F. Helleri*, showing two different groups of chromosomes.

FIGURE 13.—Diakinesis of the same (14 paired chromosomes).

FIGURE 14.—Homeotypic metaphase of the same (14 chromosomes).

FIGURE 15.—Root-tip cell of the $F_2$ plant of *F. bracteata*×*F. Helleri*, showing 28 somatic chromosomes.

FIGURE 16.—Diakinesis of reduction division of $F_1$ of *F. bracteata*×*F. virginiana* showing 7 bivalents and approximately 21 univalents.

FIGURE 17.—Metaphase of the same.

FIGURE 18.—Early metaphase of the same,—univalents lagging behind.

FIGURE 19.—Late anaphase of the same.

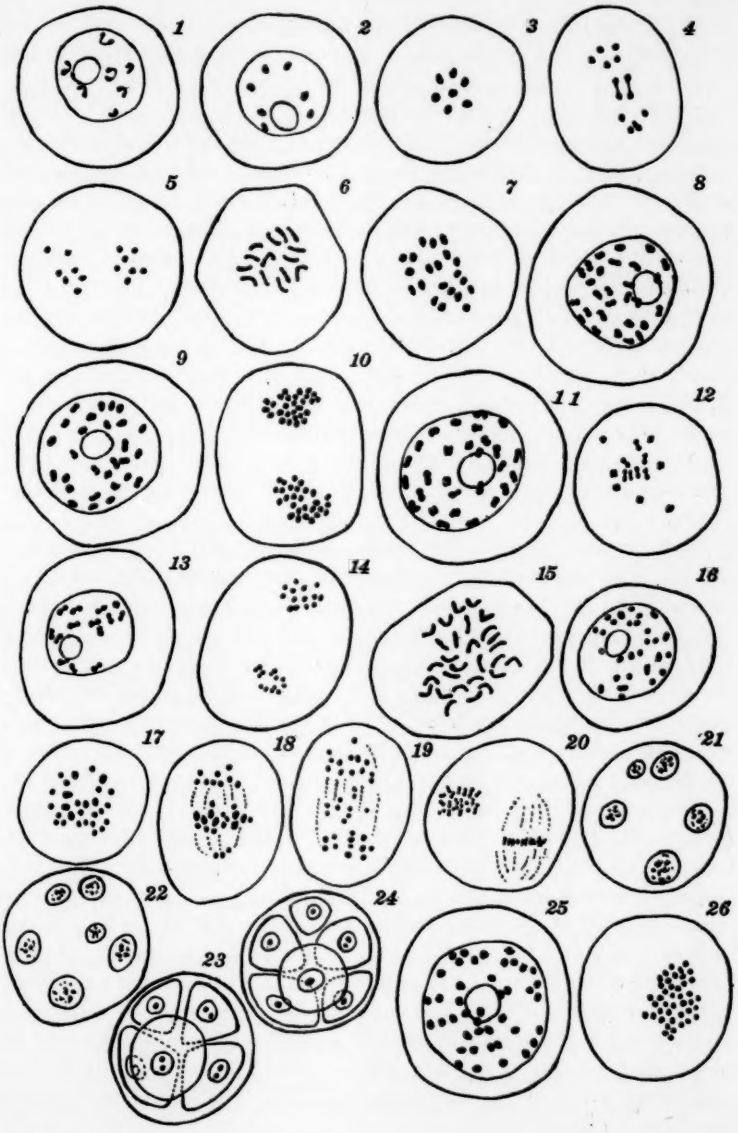
FIGURE 20.—Homeotypic metaphase of the same.

FIGURES 21–24.—Abnormal tetrad formations of the $F_1$ of *F. bracteata*×*F. virginiana*.

FIGURE 25.—Diakinesis in *Duchesnea indica*.

FIGURE 26.—Metaphase of the same.

*Plate I*



f. *Chromosomes in $F_1$ hybrids*

$F_1$ hybrids between species of the European type, such as *F. vesca*×*F. Helleri*, *F. vesca*×*F. americana*, *F. Helleri*×*F. americana*, and *F. bracteata* ×*F. Helleri* possess 7 pairs of chromosomes. Ordinarily there is no irregular behavior of the chromosomes, but an interesting exception has been found in the $F_1$ of one such cross. An individual in one of the populations of $F_1$ hybrids between *F. bracteata*×*F. Helleri* was found showing 14 pairs of chromosomes (figure 13) in the diakinesis of the pollen mother cell. Presumably the 7 chromosomes contributed by the bracteata parent and the 7 chromosomes contributed by the *Helleri* parent had doubled during some abortive attempt at cell division. Figure 12 shows one group of 7 chromosome pairs in the heterotypic metaphase which is easily distinguishable from a second group of 7 chromosome pairs. In the homeotypic division 14 chromosomes as a haploid number may be counted clearly (figure 14). The behavior of the gametic chromosomes seems to be normal. The $F_2$ hybrids obtained by selfing this plant showed 28 chromosomes in root-tip preparations (figure 15). The writer has not been able to investigate conditions in the pollen mother cells of the $F_2$ plants.

In $F_1$ hybrids between the species of the American type, for example *F. glauca*×*F. virginiana*, no abnormal chromosome behavior was observed. But hybrids between species of the different types, for example American type ($x=28$)×European type ($x=7$), which can be obtained only with difficulty, show many irregularities. Among a population of $F_1$ hybrids between *F. bracteata*×*F. virginiana* some individuals were found having 28 chromosomes in the heterotypic metaphase, of which 7, presumably bivalents, appear to be larger than the other 21 (figure 17). In the early metaphase there are approximately 28 chromosomes of which 7 bivalents are on the equatorial plate, while 21 univalents are found on the spindle (figure 18). Figure 19 shows 7 bivalents which, having divided, are pushing toward the poles, while the 21 univalents are lagging in their approach to the poles. It is obvious that each of the bivalents divides before moving to the poles, but the univalents pass at random to either pole without dividing. Owing to the minute size of the chromosomes, it is quite difficult to count the number of the bivalents and univalents in the heterotypic division. In figures 21–24 one may observe clearly the irregularity of the tetrad formation, a consequence to be expected from the previous behavior of the chromosomes. This irregularity of tetrad formation supplies the cytological basis of the practically complete sterility of these hybrids.

## DISCUSSION

### a. *Polyploidy in Fragaria species*

The foregoing investigation gives us another case of possible polyploidy in plant species. If the basic haploid chromosome number is taken to be 7, various Fragaria species may be interpreted as diploid, tetraploid, hexaploid and octaploid forms, that is, as forms having 7, 14, 21 and 28 pairs of chromosomes. Furthermore, *Duchesnea indica*, which once was classified as a species of Fragaria is found to have 42 pairs of chromosomes; and since it may be crossed with *Fragaria vesca*, it may possibly be regarded as a dodecaploid Fragaria (figures 25, 26).

The occurrence of chromosomes in a progressive arithmetical series has been found in several other genera. In Chrysanthemum TAHARA (1915, 1921) found species with haploid chromosome numbers 9, 18, 27, 36 and 45. In Viola, according to MIYAJI (1913) and MARCHAL (1920), there are species with 6, 10, 12, 24 and 36 haploid chromosomes. In Hieracium ROSENBERG (1917) found somatic numbers 18, 27, 36 and 54. In Crepis there are species with 6, 8, 10, 16, 18, 24 and 42 somatic chromosomes (ROSENBERG 1918, 1920). In Triticum SAKAMURA (1918, 1920) and SAX (1921, 1922) state that one species has 7 chromosome pairs, four species have 14 pairs, and three species have 21 pairs. In Campanula MARCHAL (1920) found 17, 34 and 51 haploid numbers. In Rubus LONGLEY (1924) found 7, 14 and 21 chromosome pairs. TÄCKHOLM (1920, 1922) and BLACKBURN and HARRISON (1921), investigating the genus Rosa, have established the most remarkable series with forms having 14, 21, 28, 35, 42 and 56 somatic chromosomes.

The European type of Fragaria which has the haploid chromosome number 7 may perhaps be regarded as the most primitive species of the genus. This species not only possesses the lowest chromosome number, but also its morphological characters appear to be the most primitive when compared with those of *F. elatior*, *F. virginiana*, and *F. chiloensis* which more closely resemble the horticultural varieties having higher chromosome numbers and more complex morphological characters. Furthermore the species of the European type are hermaphroditic, while certain species of the American type and of the Chilean type are partially dicœcious.

No wild species were found possessing 14 pairs of chromosomes. Evidence of tetraploidy in Fragaria, therefore, rests upon a single case obtained in the cross between *F. bracteata* (x=7) and *F. Helleri* (x=7). The ordinary $F_1$ plants obtained from this cross were intermediate

PLATE II

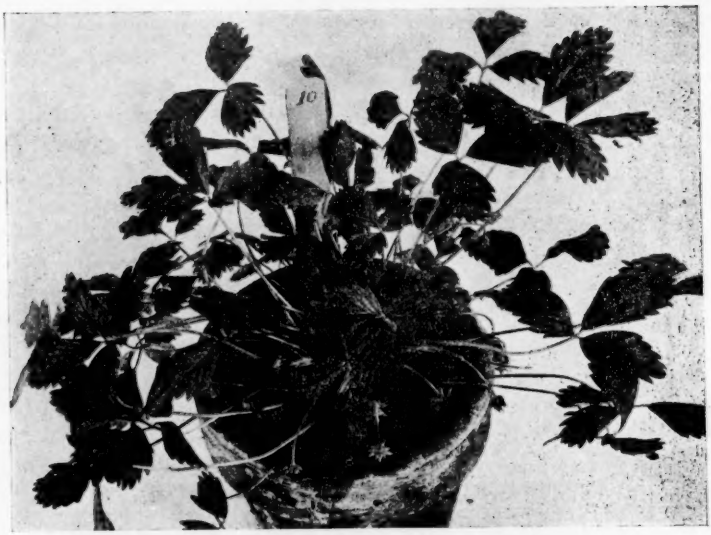



FIGURE A.—*F. bracteata*. A species of the European type.

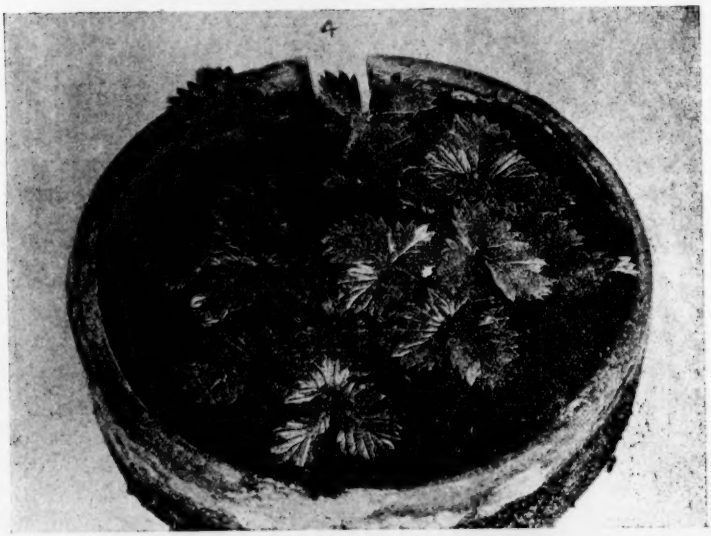



FIGURE B.—Hybrid, type b, of *F. bracteata*×*F. Helleri*.

PLATE III

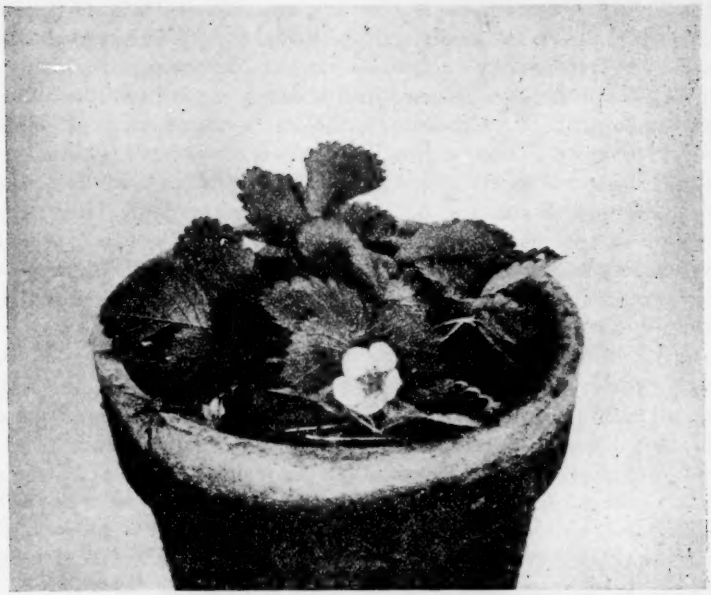


FIGURE A.—*F. virginiana*, a typical American type.

FIGURE B.—Hybrid of *F. bracteata*×*F. virginiana*.

between the parents except for flower color, the pink flower characteristic of *F. Helleri* being dominant. Nine of these ordinary hybrids (type a) were investigated cytologically and were found to have 7 pairs of chromosomes. The behavior at reduction was normal. The exceptional individual had 14 pairs of chromosomes, and instead of segregating and recombining the characteristics of the parental species as did the ordinary $F_2$ populations, it produced a uniform population of a new type. The leaves were larger, thicker and more crenate than either of the parents. The petals also were thicker and the pollen grains were decidedly larger than in the forms from which it arose (Plate 2, A and B). The root-tip cells of seven individuals were examined, and in each case 28 chromosomes were found. These plants may therefore be considered to be representatives of a new species.

Several other cases of plant tetraploidy which occurred under observation have been reported. *Oenothera gigas*, a mutant form of *O. Lamarckiana*, is a well known case (LUTZ 1907). In Primula DIGBY (1912) found a tetraploid form with 36 somatic chromosomes, and in Datura a tetraploid form has been found which has 48 somatic chromosomes instead of the 24 of the original species (BLAKESLEE, BELLING and FARNHAM 1920). In Nicotiana, CLAUSEN and GOODSPEED (1925) produced a true-breeding hybrid between glutinosa ($x=12$) and tabacum ($x=24$) which possessed 36 pairs of chromosomes.

### b. *Species hybrids*

In the $F_1$ hybrids of *F. bracteata* ($x=7$)$\times$*F. virginiana* ($x=28$), as previously stated, there are 7 bivalents and 21 univalents in the heterotypic spindle. In the reduction division the bivalents divide normally while the univalents pass at random, without dividing, to either pole. The behavior of these chromosomes in the second division has not been clearly observed. But the subsequent tetrad formation seems to be much disturbed, because the majority of the pollen mother cells form three, five or six daughter nuclei instead of the normal four, none of which are able to become normal mature pollen grains. The irregularities of the chromosome behavior show the cytological basis of the sterility of the hybrid. This view has been borne out in several other species hybrids (See Plate 3, A and B).

Similar chromosomal irregularities in the heterotypic division of hybrids have been investigated in many other species. In Drosera ROSENBERG (1909) has investigated a hybrid between a species with 10 haploid and a species with 20 haploid chromosomes which shows

10 bivalent and 10 univalent chromosomes at diakinesis. GATES (1909) found the chromosome number of the $F_1$ of certain Oenothera crosses to be 20 or 21, the sum of the gametic number of the parents. In an $F_1$ hybrid of *Hieracium auricula* (x=9)×*H. aurantiacum* (x=18), 9 bivalents and 8 or 9 univalents were found in the reduction division (ROSENBERG 1917). In Triticum KIHARA (1919) described 14 bivalents and 7 univalents in the heterotypic prophase of the $F_1$ hybrid *T. polonicum* (x=14) ×*T. spelta* (x=21). YASUI (1921) found a similar chromosome behavior in Papaver hybrids. TÄCKHOLM (1920, 1922) found that species of the Canina section in Rosa have usually 7 bivalents with 14, 21 or 28 univalents in the reduction division. SAX (1922) reports that in the $F_1$ of *Triticum monococcum* (x=7)×*T. turgidum* (x=14), there are 7 bivalents and 7 univalents in the heterotypic division; and the $F_1$ of the Emmer group (x=14)×the Vulgare group (x=21) shows 14 bivalents with 7 univalents in the first meiotic division, resulting in microspores having from 14 to 21 chromosomes.

## SUMMARY

1. The Fragaria species investigated may be divided according to their chromosome number into four groups having 7, 14, 21, and 28 chromosomes respectively.

2. $F_1$ hybrids between different representatives of the American type have 28 gametic chromosomes.

3. $F_1$ hybrids between different representatives of the European type have 7 gametic chromosomes, with the exception of the following case.

4. The cross of *F. bracteata*×*F. Helleri* produced, in one case, a tetraploid form, having 14 gametic chromosomes, of which 7 are contributed by one parent and 7 by the other parent. The $F_2$ plants which were obtained by selfing this tetraploid form have 28 somatic chromosomes in the root-tip cells, and possess distinct morphological characteristics which have not been observed in any other species. The type may be regarded as a new species.

5. In the $F_1$ hybrid of *F. bracteata*×*F. virginiana* 7 bivalents and approximately 21 univalents were found. The bivalents divide normally, but the univalents pass at random to either pole without dividing. The tetrad formation seems to be greatly disturbed, consequently there are no normal mature pollen grains found.

6. *Duchesnea indica* is found to have 42 gametic chromosomes; and judging from possibility of crossing with *F. vesca*, it may possibly be considered to be a dodecaploid form of Fragaria.

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All drawings were made with the aid of the camera lucida. All figures were drawn from single sections. The lenses used were a 1.5-mm. Zeiss apochromatic objective and a No. 10 compensating ocular.

# FURTHER EVIDENCE ON THE FACTOR FOR BITTERNESS IN THE SWEET ALMOND

MYER J. HEPPNER

*Division of Pomology, University of California, Davis, California*

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In the July 1923 issue of GENETICS in an article entitled "The Factor for Bitterness in the Sweet Almond," the writer presented data from an almond breeding experiment started in 1916 which seemed to show that as far as their genetic constitution for bitterness and sweetness is concerned, all varieties of sweet almonds are hybrids. This assumption was based on the fact that out of 243 seedlings derived by crossing different varieties of sweet almonds which came into bearing in 1922, 184 possessed sweet nuts and 59 possessed bitter nuts, or in terms of four in the ratio of 3.028 : 0.972, a very close approximation to the theoretical Mendelian monohybrid ratio of 3 : 1.

Since the report referred to above was first made, 480 additional trees have come into bearing so that at the present time data are available from a total of 723 trees. The following table shows the crosses made and the number of trees bearing sweet or bitter nuts in each cross:

| Cross | | | *Sweet trees* | *Bitter trees* |
|---|---|---|---|---|
| Lewelling | × | IXL | 21 | 4 |
| California Paper Shell | × | Nonpareil | 20 | 5 |
| Ne Plus Ultra | × | Drake | 2 | 0 |
| Ne Plus Ultra | × | IXL | 34 | 10 |
| Nonpareil | × | Peerless | 9 | 4 |
| California Paper Shell | × | IXL | 4 | 5 |
| Lewelling | × | Ne Plus Ultra | 5 | 3 |
| California Paper Shell | × | Ne Plus Ultra | 2 | 1 |
| Reams | × | Ne Plus Ultra | 5 | 1 |
| Nonpareil | × | California Paper Shell | 27 | 6 |
| Reams | × | California Paper Shell | 8 | 0 |
| Nonpareil | × | Texas | 21 | 4 |
| Nonpareil | × | Ne Plus Ultra | 13 | 8 |
| Drake | × | Jordan | 7 | 0 |
| Drake | × | Ne Plus Ultra | 43 | 17 |
| Reams | × | Nonpareil | 4 | 3 |
| Reams | × | IXL | 2 | 2 |
| Languedoc | × | Drake | 14 | 7 |
| Reams | × | Texas | 5 | 3 |
| Ne Plus Ultra | × | Lewelling | 29 | 6 |
| Drake | × | IXL | 23 | 5 |
| California Paper Shell | × | Jordan | 9 | 0 |

| | | | | |
|---|---|---|---|---|
| Ne Plus Ultra | × | Harriott | 12 | 0 |
| Lewelling | × | Nonpareil | 4 | 0 |
| Nonpareil | × | IXL | 17 | 7 |
| I×L | × | Ne Plus Ultra | 7 | 4 |
| King | × | Ne Plus Ultra | 10 | 0 |
| Drake | × | Languedoc | 9 | 1 |
| Nonpareil | × | Drake | 13 | 12 |
| Ne Plus Ultra | × | Nonpareil | 17 | 7 |
| Drake | × | Peerless | 19 | 14 |
| Languedoc | × | Ne Plus Ultra | 2 | 1 |
| Peerless | × | California Paper Shell | 1 | 0 |
| Golden State | × | Sellers | 2 | 0 |
| Drake | × | Texas | 25 | 4 |
| Drake | × | California Paper Shell | 51 | 13 |
| Texas | × | Drake | 2 | 2 |
| California Paper Shell | × | Drake | 15 | 7 |
| Harriott | × | Big White Flat | 10 | 0 |
| Nonpareil | × | Eureka | 4 | 0 |
| Drake | × | Eureka | 2 | 0 |
| Sellers | × | Drake | 3 | 1 |
| Lewelling | × | California Paper Shell | 5 | 3 |
| Ne Plus Ultra | × | California Paper Shell | 3 | 2 |
| I×L | × | Reams | 2 | 1 |
| Languedoc | × | IXL | 1 | 0 |
| | | Total | 547 | 176 |

An examination of the above table shows that there is no uniform outstanding proportion between trees possessing sweet almonds and those possessing bitter almonds in all the crosses. However, when the totals are examined, it will be noticed that there is nearly a perfect 3 : 1 ratio, the actual ratio being 3.108 : 1. It will also be observed that in only one case are there more bitters than sweets; namely, in the California Paper Shell×IXL cross in which 5 trees out of 9 possess bitter nuts. It will also be seen that in some of the crosses no bitter nut bearing trees have appeared.

With the larger population of trees available for study the assumption made in the first report that all sweet almonds are probably heterozygous for sweetness as the dominant character and the factor for bitterness as the recessive seems to be substantiated with the possible exceptions of the case mentioned above and the two crosses having the Harriott as one of the parents, in one case Na Plus Ultra×Harriott and the other Harriott ×Big White Flat in neither of which any bitter nut trees appeared. The total of twenty-two individuals in these two crosses, all of which possess sweet nuts is a fairly good indication that Harriott is possibly homozygous for sweetness.

# INDEX

Prepared with the assistance of MR. JACK SCHULTZ, graduate student, COLUMBIA UNIVERSITY. Page numbers printed in black-faced type refer to headings of articles or sections. Numbers in italics indicate references in lists of "Literature Cited."


ABDERHALDEN, E. 178, *198*
Abdominal bands 489
ABEGG, F. A. 163
Aberrant ratios 433
Ability in human stock 568
Abnormal types of gametes 153
Abnormalities in chromosome distribution 267
  Morphological 489
Accessory factor causing differential rate of pollen tube growth 433
Acid hydrolysis 181
Adaptation, theory of 300
Adoxaceae 74
*Aegilops cylindrica* 328
AGAR W. E. *371*
Age of parents 282
Agouti, allelomorph series 463, 464
  Color 532
ALBERTS H. W. 235
Albinism 457
Albino 295
ALDER, B. 91, 124, *125*
Aleurone 5
Algae 74
  Injured by low temperature 85
Allelomorph 463,556, **557**, **563**, **567**, 568
  Agouti factor 464
  Black extension factor 461, 464
  Presence of normal 484
Allelomorphic series 479
  Sterility factors 480
Allelomorphism 506
ALLEN, C. E. **83**, 85, 86, *87*, 452, *454*, 592, *602*
Allen's modification of Bouin's solution 128
Almond 74
  Bitterness in 605
ALTENBURG, E. 5, *26*, 485, 489, *502*
Amylase 177, 184
  Hydrolysis 181–184
  Produced during germination 187
Amylodextrin 192
Amylopectin 178
  Polymerized 194
Amylose 178, 179
  Polymerized 194
Anaphase, heterotypic 135
ANDERSON, E. S. 472, 473, *481*
Angiosperms 74, 452
Animals, factorial formulae of 463
Anther loculi, orientation of spindles in 269
Antirrhinum 188
Apigenin 188
Apple 74, 80
APOLANT 300
Apotettix 5
Apricot 74
Archegoniatae 74
Archesporial cell 271
  Stage 128
ARMSTRONG, E. F. 189, 193, *198*
Arrowroot, starch 194
ASHMEAD 305
Assortment of male gametes at fertilization 447
BABCOCK, E. B. 602
Backcross, alternated 50, 53, 54
  Xple 50
BACKHOUSE, W. O. 317, *332*
Bagg albino strain 295
BAITSELL, G. A. 584, *589*
BAKER, J. C. 178, 192, 194, *199*
Balanced lethals 69
  Muller's hypothesis of 68, 71
BALL, E. D. 91, 124, *126*
Banana culture-medium 291
Barley diastase 194
Barley starch 194
BASHFORD 300
Basic chromosome number 317
BATESON, W. 5, *26*, *293*
Bateson, presence-and-absence hypothesis 165
Batrachoceps 268
BEAN, ACHSA 309
BEER, R. *602*
Beet 75, 80
BELLING, J. 276, 277, *278*, 600, *602*
BENNETT, A. A. 539, *583*
BERGHS, J. 268, *278*
Bessel's formula 15
*Beta vulgaris* 75, 80
BIEDERMANN, W. 178, *198*
BITTENBENDER, H. A. 356, *371*
Bitter orange 74
Bitterness in almond 605
Bivalents 320, 322, 323, 327
Black rat **456**, 464
BLACKBURN, K. B. 597, *602*
BLAKESLEE, A. F. 89, 95, *126*, 276, *278*, *354*, 600, *602*
BLARINGHEM, L. *602*
BOEDIJN, K. 145, *162*, 231, *234*, *354*
BONNIER, GERT 490, *502*
BOOTH, N. O. 388, 392, *402*
Bouin's solution, Allen's modification of 128
BOURQUELOT, E. 178, *198*
BOWEN 300
BOYCOTT, A. E. 483, *502*

Breeding contest, international egg laying and 123
BREGGER, T. J. 5, *26*, 414, *422*
BREITENBECHER, J. K. 348, *351*
BRIDGES, C. B. 3, *26*, **41**, **43**, **44**, *56*, **249**, *266*, 277, *279*, 280, *293*, 348, *351*, 485, 491, 493, *502*, **503**, 504, 506, 509–513, 515, 516, *530*, 585, *589*
BRIEGER, F. G. 451, *454*
BRINK, R. A. **38**, *40*, **163**, 165, 188, *198*, 407, 411, 414, 418, 420, *422*, 445, 448, 451, *454*
Bristles 510
BROOKE, H. C. 458, 462
BRUCHUS 348
BRÜCKE, E. 191, *198*
BRUNSON, A. M. 235, *248*
Bud pollinations 468
  Mutations 348
BUNYARD, E. A. *602*
California 510
Campanula 597
Canna 267, 276
Carbohydrate 163
  Effect of the waxy gene on 196
  Grains, endosperm of maize 409
  Grains, pollen 409
  Metabolism 166, **451**
  Reserve 166
    Endosperm and pollen 163
    Starchy pollen 420
    Waxy endosperm 445
    Waxy maize 196
  Segregation of 407
  Separation of 167
  Stereoisomeric forms of 79
CASTLE, W. E. 5, *26*, 336–338, 349–351,458, 532, *583*
*Cavia cutleri* 334
Cell
  Archesporial 271
  Fertilization of a tetraploid by a diploid 275
  Heterotypic metaphase 140
  Megaspore mother 268, 273
  Pre-diakinesis stage 272
CHAMBERLAIN, C. J. 273, *278*, 330 *332*
Changing over toward wild type 250
Characters
  Fixed by consitituion of mother 483
  Which distinguish subspecies 463
Chemical composition
  Pollen and endosperm starches 177
  Pollen and seed 166
Chenopodiaceae 75
Chinch-bug 7, 374
Chinese maize 410
Chromatin strands, parallelism of 322
Chromogens 189
Chromomeres 132
Chromosomal cohesions 202
Chromosome **41**, 250, 257, **320**, 325, **592**
  Arrangement into circles 149
  Arrangement, irregularity in 138, 160
  Arrangement, regular zigzag 138, 151
  Attraction 160
  Basic number 317
  Behavior 154, **317**
  Circles 135, 149
  Complex 152
  Distribution, abnormalities in 267
  Exchange 154, 157, 160
  Failure to pair 147
  Incompatibility 148
  Lethals 227
  Map of *Drosophila melanogaster* 504
  Number of tomato 269
  Pair 202
Chromosomes 150, 324
  Cohesion of non-homologous 230
  Crossovers due to aberrant distribution of 232
  Definite sequence 159
  Differentiation of individual 133
  Expansion of 142
  Homologous 138
  Incompatible 159
  Lagging 275
  Longitudinal split 322
  Loss of 345
  Metaphase, irregularity in 139
  No pairing between homologous 134
  Nuclear changes 273
  Radiating loops 133
  Regular and uniform arrangement 138
  Reticulate condition 144
  Rye 320
  Separation 138
  Typical diakinesis 270
  Undergo process of elongation 144
  Unit in heredity 149
  Wheat 320, 328
  With affinities for each pole 150
  Zigzag arrangement 138, 151
Chrysanthemum 597
Circles, arrangement of chromosomes in 149
  Chromosomes 135
  Univalent chromosomes 158
Cinnabar 493
Citrus 74, 80
  *aurantium* 74
  *decumana* 74
  *limonum* 74
  *nobilis* 74
  *vulgaris* 74
CLAUSEN, R. E. 249, *266*, *293*, *354*, 485, 600, *602*
CLELAND, R. E. **127**, 128, 144, *162*, 202, 230, 232, *234*
CLEMENTE, L. S. 3, 4, *27*
Clones, variable 86
Coat pattern, guinea pig **333**
  Mutational mosaics 335
  Somatic and germinal mosaic **336**
Coefficient of variability 7
Cohesion of chromosomes 230
Cohesions, chromosomal 202
Coiling in the snail 483
Coix 411
*Coix lachryma-jobi* 191
COLE, MARGARET 166

COLLINS, G. N. 165, 198, 235, 248, 407, 418, *422*, 445, *454*
COLLINS, J. L. 249, *266*, 328, *332*, *602*
Color analysis 359
  Guinea pigs 334
  Pattern in fowl 357
  Rat 456
Color reactions of starches with iodine 177
Color segregation, ratios in 448
Color type 459
Color types of skins 460
Coloration of black rat 458
Combinations, factorial 86
Committee on genetic form and nomenclature 214
Compatible matings of self-sterile Nicotianas 467
Complementary factors 213
  Class, mortality of 48
  Classes, ratios of 49
  Factors for flower color 189
COMPTON 466
Configurations in triploid 274
Conglutination reaction 78
Corn 333, 423
Correction curves 55
Correlation 10, 89, 96, 97, 117, 121, 122
  Consistency of coefficients 124
  Crossover percentage 13
  Formula involving 93
  Inter-annual 91, 97
  Inter-mensual 91, 96,
  Intra-annual 91, 92, 96, 97
Correlation coefficients 91, 97, 98, 100, 104, 124
  Differences 104
  Distribution of magnitudes of inter-mensual 89, 105–116
  Egg production 89, 92, 123
  Inter-mensual 93
  System of 123
CORRENS, C. 433, 451, *454*
COULTER, J. M. 273, *278*, 330, *332*
COULTER, M. C. 448, 449, *454*
Coupling 237
Coupling phase 238, 240, 241
Cowpea weevil 348
CRAIG, A. G. 388, *402*
CRAMER, 300
CRANE, M. B. 388, 393, *402*, *602*
Crepis 328, 597
CREW, F. A. E. 457, 459, *465*
Crossing over 3, 9, 19, 41, 42, 44, 133, 154, 161, 231, 493
  Between members of a trisomic set 267
  Between three sets of genes 277
  Combinations of 439, 441
  Effect of environmental and genetic factors 44
  Formulae for finding the percentage of 240, 241
  In maize 1
  In X chromosome 54
  Increase or decrease in 19
  Increases tumors 255
  Interchromosomal 154, 157
  Modifiers of amount of 48
  Percentage 11, 243
  Values 440
  Variation in 3, 15, 16
Crossover, data 28, 30, 36, 37
  Percentage 2, 4–6, 15, 17–25
    Apparent 314
    Correlation of 13
    Fluctuations in 21
    Genetic 314
    In male and female gametes 13, 32
    In male gametes 7
    Tomato 392, 393
    Variability of 8, 10, 11
    Variations 12
Crossovers due to aberrant distribution of whole chromosomes 232
Cross-sterile 466
Cryptomeres 357
CUÉNOT, L. 451, *454*
CUMMING, M. B. *602*
Curly 491, 495, 496
Curved 491
Curves 54
  Correction 55
Cytological studies on Fragaria 590
Cytoplasm 500
Cytoplasm during meiosis 269
CZAPEK, F. 178, *198*
DARROW, G. M. 590, *602*
Datura 267, 276, 354, 600
DAVENPORT, C. B. 276, *278*
DAVIS, B. M. 57, 58, 65, *72*, 127, *162*, 212, 230, *234*, 277, *278*, *602*
Deficiency
  Females 489
  Recessives 211
  Splitting progenies 211
DEMEREC, M. 38, 165, *198*, 407, 411, *422*, *445*, *454*
DETLEFSEN, J. A. 3, *26*, *27*, 464, *465*
Deviations from
  Dihybrid distribution 237
  Expected ratios 420
  Normal ratios 217, 438, 439
Dextrin 166, 168, 169
Diakinesis 133, 135, 145, 147, 270, 276, 353
  Trisomes in early 272
Diastase, barley 194
DIETRICH, Kathleen 166
Differential pollen tube growth 429, 430, 433, 448
Differentiation of individual chromosomes 133
DIGBY, L. 144, *162*, 600, *602*
Digestion of endosperms 187
Dihybrid 225, 534, 558
  Families, double-dominant segregates 225
  Mendelian distribution 237
  Ratios in Oenothera 225
Diploid 317
  Chromosome number 269
  Germ cell, fertilization of tetraploid by diploid 275
  Tissues 408
  Tomato 267

Diptera 276
Distribution
  Laws of 135
  Magnitudes of correlation 117
  Magnitudes of inter-mensual correlation coefficients 105–116
DIVER, C. 483, *502*
Domestic fowl 89
  Physiology of egg production 123
Dominant
  Class 208
  Factors 568, 570
  Individuals
    Disappearance 573
    Elimination 534
  Types, excess 462
  Zygotes 556
Double crossing over 42, 43, 510, 512, 521
Double dominant 225
  Backcrossed to double recessive 226
Double fertilization 1
Double recessive 214, 222
  Backcrossed to double dominant 226
  Backcrosses 229
DRINKARD, A. U. 388, 393, *402*
Drosera 600
Drosophila 1, 3, 7, 9, 267, 276, 348, 584
  Bar flies, distribution of tumors to 264
  Bar × tumor 264
  Chromosome map 504, 527
  Crip-h 281, 285, 292
    Factor 291
    Flies in high-temperature 283
    Legs, forms exhibited by 282
  Crip-m 281, 286, 290, 292
    Flies, median legs of 289
    Locus of 291
      Origin and description of 286
  Crippled 280
    Two types 281
  Death
    Female 499
    Female zygotes 482
    Rate 500
  Dichaete 249, 250, 254, 260, 285, 493
  Distribution of tumors 264
  Doubling of middle leg 287
  Egg characters in 484
  Eye color factors 213
  Eyeless 264
  *funebris* 490
  Gynandromorphs 348
  Inheritance of crippled 280
  Linkage relations of tumor in 249
  *melanogaster* 292, 482, 484, 490, 501, 503, 504, 505, 507
  Mutant characters 250, 503, 529
  Purple 491
  *simulans* 490, 501
  Star 249, 254, 285, 491
  Tumor, linkage relations 249
  Vestigial wing 584
  *virilis* 584, 585, 588
  Wing length 586
*Duchesnea indica* 601
DUFF, CECIL 391
DÜLL, G. 191, *198*
DUNN, L. C. 356, 358, *371*
Dwarf stature 58
  Trisomic inheritance 352
Dwarfs, hypothesis for 69
Dynamics, waxy gene 163
EAST, E. M. 1, 3, *27*, 433, 451, *454*, 466, 478, *481*, *602*
EATON, O. N. 333
EGBERT, A. D. 91, *125*
Egg 500
Egg characters
  *Drosophila melanogaster* 484
  Silkworm moth 483
Egg laying contest 90, 123
Egg production
  Correlation coefficients 123
  Correlation individual months 92
  Domestic fowl 123
  Inter-annual correlations 97
  Inter-mensual correlation 89, 96
  Intra-annual correlation 96
  Laws concerning 90
  Months of first laying year 90
EHRLICH 300
Einkorn 328
ELDERTON 394
Elimination
  Individuals 534, 557, 563, 567, 568, 570
  Old-gold type 208
Elongation of chromosomes 144
Embryo 500
  Malnutrition 71
Embryo-sac mother cells reduction division 273
EMERSON, R. A. 3, 5, 6, 15, *27*, 235, 243, *248*, *351*, 372, 373, 385, *386*, 433, 437, *454*
EMERSON, S. H. 128, *162*
Empetraceae 74
Emulsin 194
Endonucleolus 129 132, 158
Endosperm 5, 7, 165, 166, 187
  Carbohydrate reserves in 163
  Characters 1
  Composition 7
  Reserve material 169, 170, 181, 184
  Seedling growth 185
Endosperm reserves during seedling development 184
Endosperm segregation,
  Both parents heterozygous 419
  Plants heterozygous for waxy 417
  Waxy maize 412–414
  Waxy maize fertilized by segregating pollen 413
  Waxy × starchy maize hybrids 415, 416
Endosperm starch 177, 196
  Crude amylose in 179
Endosperm, sugary 433
Environment 491
  Effect on variegation pattern in maize 372, 375
  Influence of 282
Environmental agencies, effect upon crossing over 44

Enzyme activity 166
Enzyme formation 189
Eosin 485, 486
Equatorial plate 321, 324
Ericaceae 74
Erythrodextrin 166, 191, 407
Evening primrose 201
Extension
  Allelomorphs 463
  Melanic pigment 358
  Series 463
Eye 457, 489
  Color factors of Drosophila 213
  Reduction in size 489
Eyeless 264
  Percentage of tumors 264
EYSTER, W. H. 5, 15, *27*, 333, *351*, 372, 373, *386*, 443, *454*
Factor 534
  Affecting transplantation 299
  Causing deviation 420
  Complementary 213
  Crip-h 285
  Crip-m 291
  Detrimental to full expression of *brevistylis* 65
  Disturbing normal segregation 432
  Expression of 65
  Flower color 189
  Habrobracon 314
  Independent dominant 567
  Influencing waxy ratio 446
  Old-gold flower color 203
  Sugary chromosome 443
Factorial combinations 86
Families
  From self-fertilized heterozygotes 209, 217
  Illustrating true-breeding 206
  Intra-sterile classes 469
FARNHAM, M. E. 600, *602*
FELDMAN, H. W. 456, 457, *465*
Female
  Deficiency 489
  Killing lethal 487
  Low proportion 485, 487
  Selection 370
  Time of death 499
Ferric chloride 4
Fertilization
  Prevented 64
  Selective 247
  Tetraploid × diploid 275
Flavones 188
FLEMMING 128
FLETCHER, S. W. *602*
Flies, 1, 4, 8, 510, 523
  Distribution of tumors 264
Flower color
  Complementary factors 189
  Old-gold 201
  Types in Oenothera 216
Flowering plants, gametophyte in 166
Fluctuations
  Crossover percentage 21
  Sampling 12
Food 284
  Larval 281
Forked 485
Formula
  Correlation of two systems of correlation coefficients 93
  Homozygous old-gold 214
  Homozygous sulfur 214
  Homozygous yellow 214
Formulae
  Measuring linkage intensities 236
  Percentage of crossing over 240, 241
  Relation of different members of phenotypic series 239
  Value of any member of gametic or phenotypic series 239
  Value of n 238
Fowl
  Application of theory to breeding practices 369
  Barred Rocks 356
  Brown Leghorn 356–358, 369
  Buff Leghorn 358
  Columbian pattern 370
  Correlation egg production 89, 121
  Gene restricts pigment 356
  Genetic constitution 357
  Genetic formulae 360, 361
  Inheritance of plumage color 355
  Jungle 358, 369
  Orpington 358
  Pattern factor 356
  Recessive white 357
  Restriction factor 357
  Rhode Island Red 355–358, 369, 370
  Sex-linked color pattern 356
  Standard color 368, 369
  Standard of perfection 355
  White of several genotypes 369
  White Plymouth Rock 357
  Xanthic factor 356
Fractional sterilization 76
Fragaria 590
Fragaria species, polyploidy in 597
Frequency of tumors 250
FRIEDENTHAL, H. 73, *82*
FRIMMEL, F. 388, *402*
FROST, H. B. *354*
Fruit fly 8
GAIRDNER, A. E. *602*
Gamete 5
  Abnormal types 153
  Crossover percentage in male 7
  Crossover percentage, male and female 32
  Differential viability 237
  Lethal 215, 217, 226
  Method of deriving 564
  Shifting 565, 576
  Viability 237
Gametic generations 534
Gametic proportions 557
Gametic series 236
  Corresponding phenotypic series 236
  Formulae 239
Gametophyte
  Factor 443, 445, 449

Gametophyte (continued)
Factor in waxy stock 448
Flowering plants 166
Generation 452
Genetic factors affecting 453
Mendelian factors in maize 423
Gametophytic inheritance, sphaerocarpos 83
Gametophytic offspring 84
Gametophytic progeny 83
GASIS, D. 73, *82*
GATES, R. R. 230, *234*, 276, 277, *278*, 327, *332*, *602*
GATES, W. H. 458
GEERTS, J. M. 276, *278*, *602*
Gene 255, 266
Dynamic properties 164
Effect of waxy, on carbohydrate reserve 196
Elements 373
Independent 402
Influences rate of pollen tube growth 430
Locus main third-chromosome 258
Locus tumor 261, 262
Modifying 491
Mutation 204, 205
Nine pairs in six groups 401
Tumor 250, 257
Waxy, 38
Genes
Complementary 491
Crossing over between three sets of 277
Laws of independent assortment 146
Within chromosome pair 202
Genetic agencies, effect upon crossing over 44
Genetic composition
Defective plant 431
*Oenothera biennis* 148
Genetic constitution, host 302
Genetic form and nomenclature committee 214
Genetic relationships 394–399, **461**
Genetic uniformity, typical clones 83
Genetical formulae 66, 67
Genetical significance, irregularities in chromosome behavior 154
Genus cross 328
Germinal causes, linkage variations 4
Germinal changes, related species 465
Instability 351
Mosaic in guinea pig 349
Germinate, failure of seeds to 237
Germination 60
Amylases produced during 187
Percentage 59
Seeds forced to complete 58
GILBERT, A. W. 388, *402*
Gnetales 74
GOHLKE, K. 74, 78, *82*
Gold Nugget 423, 425
Golden Bantam 433
GOLDSCHMIDT, R. 484, *502*
GOODALE, H. D. 90, *126*, 356, 357, *371*
GOODSPEED, T. H. *354*, 600, *602*
GORTNER, R. A. 189, *198*
GOWEN, J. W. 3, 4, 5, *27*, 44, *56*
GOWEN, M. S. 4, 44, *56*
Grafting, precipitin reaction 73
Grapefruit 74
Grass 191
GREEN, F. 73
GREGORY, R. P. *603*
GRIS, A. 191, *198*
GROTH, B. H. A. 388, *402*
Growth
Curves 477
Pollen 64
Pollen tubes **63**, 70, 71
Weight of seed residues during 186
Guinea pig **333**, 348, 532
Guttermann's method 76
GUTTMANN, F. 74, *82*
Black-eyed golden agouti 334
Black-eyed golden agouti with 7 dominant factors, type 334
Breeding record 339
Color 344
Color factors 334
Formulae of ancestors of mosaic 337
Germinal mosaic 349
Inbred strains 333
Mosaic **342**, **344**
Mosaic germinal and somatical **336**, 338
Mutant 351
Piebald 333
Somatic mosaics 350
Somatic mutations 333
Spots 350
Tortoiseshell 333
Tortoiseshell, genes for 333
Gymnosperms 74
Gynandromorphs, in Drosophila 348
Gypsy moth 484
HAALAND 300
Habit 58
Habrobracon
Black sooty 309
Black sooty × orange-eyed yellow 311
Crossing effect on defective and sooty 311
Defective linkage 310
Defective venation 309
Defective venation in Lancaster material 305
Defective venation, origin of 306
Defectives in second generation 309
Defectives, ratios of 305
Females, from unfertilized eggs 307, 308
First linkage group, Chromosome I 306
Formulae for parental crosses 314
Freaks 308
High defective males from crosses involving 313
High defective stocks 306
Inbreeding, effects on defective and sooty 311
Iowa City material 307
L material, differences from 307
L orange-eyed normal crossed with I 309
Lancaster material, defective venation in 305
Lethal factor 307
Linkage, evidence of 313

Habrobracon (continued)
Linkage, high defective and sooty 312
Linkage, orange sooty and defective absent 310
Low defective, segregating relationships of 311
Modifier 307
Mutation 305
Orange eye color 306
Orange-eyed low defective 309
Orange, linkage 310
Orange, males from crosses involving 313
Orange, segregating relationships of 311
Patrocliny, production of 307
Plus modifiers of 307
Primaries and secondaries 308
Prothoracic wing 307
Radius vein 305
Second linkage group 306
Selection, effect on defective and sooty 311
Sex-linkoid type 305
Sex-linkoid type, inheritance 305
Sooty, linkage 310
Sooty, males from crosses involving 313
Sooty mesosternum 308
Sooty, segregating relationships of 311
Supernumerary factors 314
Thelytoky 308
Variable characters, heredity of 305
Wing, prothoracic 308
*Habrobracon juglandis* 305
HADLEY, P. B. 358, *371*
HAGEDOORN, A. C. 457, *465*
HAGEDOORN, A. L. 457, *465*
Hairless 257
Hairy 493
HALDANE, J. B. S. 235, *248*, 440, *454*, 533, *583*
HALSTED, B. D. 388, *402*
HANNAS, R. R. 91, *126*
Haploid 320
Chromosomes 317
Number, rye 317
Tissue 408
HARRIS, J. A. **89**, 90, 95, 123, 124, *126*
HARRISON, J. W. H. 597, *602*
HARRISON, WILLIAM 193, *198*
HARTMANN, A. F. 167, *199*
HAUBER, U. A. 312, *316*
HAYES, H. K. 372, *386*, 433, *454*
HAYS, F. A. 355
HEALD, P. C. 458
HEDRICK, U. P. 388, 392, *402*
HELBORN, O. *603*
HEPPNER, M. J. 605
Heredity
Habrobracon 305
Heterozygous chromosomes in 149
Selective pollen tube growth 466
HERIBERT-NILSSON, N. 63, *72*, 451, *454*
Hero plant 61
HERVEY, G. W. 89
Heterotypic
Anaphase 135
Chromosomes 320
Division 317, 318, 320, 321, 323
Division absence of equatorial plate 321
Division dividing bivalents 322
Division splitting univalents 322
Metaphase 135
Metaphase, *Oenothera biennis* 140
Heterozygotes
Backcrosses 211
Tests for occurrence 210
Heterozygous chromosomes, a unit in heredity 149
Heterozygous species 148, 159, 160
Hexaploid 327
Hexose residues 195
Hieracium 597
*Hieracium aurantiacum* 601
*Hieracium auricula* 601
HINTON, M. A. C. 456, *465*
HOGE, M. A. 287, *293*
HOLMES, S. J. 485
Homoeotypic division 159, 318, 324, 325
Homoeotypic spindles 143
Homologous chromosomes 134, 230
Pairing 134, 138, 147, 155, 159
Separation 138
Homozygotes, tests for 210
Homozygous condition 478
Host
Transplantable tumor cells 294
Tumor 294, 301, 302
Human population 572
HURST, C. C. 388, *402*
HUTCHISON, C. B. 2, 5, 15, *27*, *422*
Hyacinthus 267, 276
Hybrid 317
Hybrid vigor 317, 319
Hydrolysis
Acid 181
Pollen starches 184
Polysaccharides 167
Starch 181–184
Hypericaceae 74
Hypothesis
Balanced lethals 68, 71
Mutation, appearance of dwarfs 69
Presence-and-absence 165
ICHIJIMA, K. 590
Immunization 76
Inbred strains, guinea pig 333
Incompatibility, origin of chromosome 148
Incompatible chromosomes 159
Incompatible matings, self-sterile Nicotiana 467
Independent
Assortment of genes 146, 394
Dominant factors 567
Factors **557, 563**
Genes 402
Inheritance 237, 247
Oenothera 201
Tomato 402–405
Independently segregating factors 299
Individuals
Eliminated each generation 575
Elimination of dominant 534
Elimination of recessive 563
Inferiority, recessive type 225

Influence of environment 282
Inheritance 285
  Color 456
  Color in Black Rat 461
  Crip-m 291
  Deviations from normal ratios 427
  Independent **201**, 237
  Maternal 491
  Plumage color in fowl 355
  Susceptibility to transplantable tumor **294**
  Vortex 249
  Waxy 446
Interaction, pollen tubes and tissues of styles 480
Inter-annual coefficients 123
Inter-annual correlation 91, **97**, 104
Inter-chromosomal crossing over 154, **157**
Interkinesis 139, **142**, 143, 158
Inter-mensual correlation **89**, 91, 93, 96, 98, 100, 124
Inter-mensual correlation coefficients, distribution 105–116
Internal change, genetic constitution of tumor cell 301
International egg laying and breeding contest 90, 123
Inter-relationship, law underlying 119
Intra-annual coefficients 91–93, 96–**104**, 123, 124
Intra-clonal variation 86
Intra-sterile classes **469**
Involucres 83
Iodine 38
  Color reaction 407
Iron-acetocarmine, smears in 319
Irregular arrangements in metaphase **156**
Irregularity, chromosome arrangement **138**, 139, 160
IRVINE, J. C. 193, *198*
JANSSENS, F. A. 268, *278*
JENNINGS, H. S. 533, 534, 557, 563, *583*
JESENKO, C. F. W. 329, *332*
Johns Hopkins University 538
JONES, D. F. 388, 392, 393, *402*, **420**, *422*, **423**, 433, *455*
Jungle fowl 369
KEEBLE, F. 189, *198*
KEMPTON, J. H. *27*, 414, 418, 420, *422*, **445**, 448, 450, *455*, *602*
KIESSELBACH, T. A. 38, *40*, **407**, *422*, 445, *455*
KIHARA, H. 277, *278*, 317, 318, 323, *332*, 601, *603*
KIRKPATRICK, W. F. 89, 95, *126*
KIRSTEIN, K. 74, *82*
KOMAI, Taku 280
KOWARSKY, A. 73, *82*
KRAUS, R. 73, *82*
LADEBEK, E. 356, *371*
Lagging chromosomes 275
LANCEFIELD, D. E. 513
LANGE, L. 74, *82*
Larva, food of 281
Larval pattern, transmission of 484
Lathyrus 189
Laws
  Distribution 135
  Egg production 90
  Independent assortment of genes 146
Leg, absence of 489
Lemon 74
LESLEY, J. W. 268, 275, *278*, **352**, *354*, 387, *402*
LESLEY, M. M. **267**, *278*, *354*, 388, *402*
Lethal 65, 227, 488–500
  Characteristics of 487
  Gamete 215, 217, 226
  *Oenothera Lamarckiana* 217
  Pollen 228
  Sex-limited **482**, 489
  Sex-linked 489
  Sperm 154, 221
Lethal effect 488
Lethal factors 150, 160
Lethal genes, X-chromosome 489
LEWIS, H. R. 89, 90, 95, 123, 124, *126*
LI, J. C. 484, 499
*Lilium lancifolium* 268
Limnaea 483
LINDSTROM, E. W. 6, 388, 392, 393, *402*
LING, A. 178, 193, 194, *198*
Linkage **235**, **437**, 532
  Gametophyte factor 436
  Habrobracon, evidence of 313
  Maize 441
  Oenothera 226
  Primula 5
  Tomato **387**, 392–396, 398–400
    Flesh color 394, 396–398, 400
    Foliage color 396, 397, 400, 401
    Fruit contour 395, 398, 399, 401
    Fruit neck constriction 397
    Genes, nine pairs in six groups 401
    Genetic relations 394, 396–399
    Grape cluster 393
    Leaf shape 395, 397, 398, 401
    Pink peach 392
    Pubescence of fruit skin 396
    Skin color 395–400
    Stature 394, 395
    Yellow pear 392
Linkage group I, 202, 230
Linkage intensities, measuring 236
Linkage relations, tumor 249
Linkage studies 247
Linkage values
  Calculating 235
  Relation to independent inheritance 247
Linkage variations, germinal causes 4
Linked genes, within single chromosome pair 202
LINTNER, C. J. 191, *198*
LIPPINCOTT, W. A. 357, 358, *371*
LITTLE, C. C. 214, 294, 296, *303*, *351*. 458
LLOYD-JONES, O. 356, *371*
Location of genes 41
Loci, order of 260, **526**
Loculi, anther 269
Locus
  Factor for crip-h 285
  Factor for crip-m 291

Locus (continued)
Second-chromosome tumor gene 261
Third-chromosome tumor gene 258
Tumor gene 262
LOEB, J. 584, *589*
Longitudinal pairing of threads 269
LONGLEY, A. E. 38, *40*, 165, 191, *199*, 407, 411, *422*, 445, *455*, 590, *603*
Long-styled nanella 59
Long-styled plants 62, 64
Loranthaceae 74
LOUNSBURY, J. A. 85
Luteolin 188
LUTZ, A. M. 600, *603*
*Lycopersicum esculentum* 75, **352**, 387
*Lymantria dispar* 484
LYNCH, C. J. 484, *502*
MACARTHUR, J. W. 387
MACGILLIVRAY, J. H. **38**, *40*, 165, *198*, 407, 411, *422*, 445, *454*
Magnitudes,
Correlation 117
Distributions 105–116, 123
MAGNUS, W. 73, *82*
Maize **1**, 5, 8, 25, **38**, **163**, **407**
Carbohydrate 190, 451
Changes in pericarp color 383, 384
Chinese 410, 413
Color 373, 380, **448**
Crosses
Starchy × waxy Coix 411
Waxy × starchy 407
Waxy with starchy maize and teosinte 411
Defective ratios 426 **448**
Defective seed **423**, 428
Defective seed factors and pollen tube growth 429
Defective seed type 442
Defective strain 425
Defectives excess of expectation 424
Deficiency sugary seeds 437
Deficiency, waxy seeds 445
Deviation, number of waxy kernels 420
Distorted ratios **423**, **433**, **445**
Dynamics of waxy gene 163
Environmental factors 385
Evergreen 433
Kernels **382**, **384**
Mendelian factors in gametophyte 423
Pericarp color 384
Pigment 374, 385
Pollen 38
Pollen grains 38
Pollen, segregation of 410
Seedling stage 186
Segregation 407
Selective action 443
Sex in 15
Starch, dextrin and sugars 168
Sugary endosperm 438
Sugary × pop cross 433
Tunicate ear 443
Variability of crossing over 1
Variegations 376, **379**, 385
Variegation, environmental difference 375
Maize (continued)
Variegation in pericarp 372
Waxy 196, **407**, 412, 413
Waxy and starchy carbohydrates **407**, **408**
Waxy carbohydrate, haploid tissue only 408
Waxy, carbohydrate reserve of 190
Waxy character 165
Waxy content of starch, dextrin and sugar 168
Waxy, crossed with starchy 411
Waxy endosperm, rate of digestion 187
Waxy endosperm, reserve materials **169**, 181
Waxy endosperms 187
Waxy gene **38**, 196
Waxy gene, dynamics of 163
Waxy gene, effect of 191, 196
Waxy kernels 409
Waxy pollen, composition 170
Waxy, starch grains 175
Waxy starch, hydrolysis of 181–183, 192
Male classes receiving eosin 486
Selection 370
Malnutrition
Developing seeds 58, 65
Zygotes and embryos 71
Man 532
MANGELSDORF, A. J. *454*, **466**, 478, *481*
MANGELSDORF, P. C. 420, *422*, **423**, **424**, 449, 451, *455*
MANN, M. 387, *402*
MANN, M. C. *278*, 328, *332*, 489, *502*
MANN, M. M. *354*
Map-distance 41, 45
Percentage of recombination 54
Unit of 42
Maps, X chromosome 54
MAQUENNE, L. 178, *199*
MARCHAL, E. 597, *603*
Maternal inheritance 491
*Drosophila melanogaster* 482
Mating, fortuitous 572
Matthiola 189, 354
Maturation
Diploid and triploid tomatoes 267
Tomato 268
Triploid 273
MAVOR, J. W. 4, *27*
Median legs, crip-m flies 289
Megasporangium, reduction within 273
Megaspore mother cells 268, 271
Megasporogenesis 16
Meiosis **127**, 128
Assortment of chromosomes 273
Cytoplasm during 269
Nuclear changes during 269
Nuclear changes, prophase 270, 272
Oenothera **127**, 145
Regularity, 144
Regularity, Oenothera 145
Meiotic prophase of triploid 267
Melandrium 451
Melanin pigments 190, 356
Mendelian
Character 463

Mendelian (continued)
Expectations, susceptible individuals 295
Factors 296, 452
Gametophyte of maize 423
Tumor 296
Laws, rediscoveries of 202
Ratios, sporophyte 453
Recessive character 457
Theory 208
Metaphase
Heterotypic 135
Irregular arrangements in 156
Irregularity in 139
*Oenothera biennis* 140
Tomato 353
Triploid 272
Zigzag arrangement 140
Method
Calculating linkage values 235
Deriving gametes 564
Guttermann's 76
Methylation process 193
METZ, C. W. 276, *278*
MEYER, ARTHUR 178, 191, 192, *199*
MEZ, C. 73, 74, 77, 78, *82*
Mice, ratio of susceptible 297
Microspore 150
Microsporogenesis 16
Millardet, A. *603*
Mitosis 373
MIYAJI, Y. 597, *603*
Mnemonic symbols 214
Modification, precipitin reaction 78
Modifier 488
Amount of crossing over 48
Fourth-chromosome 265
Modifying factor 292
MOHR, O. L. 44, *56*, 249, *266*, 348, *351*, 484, 490, *502*, 506, 512, *530*
Molecule, structure of starch 193
Monohybrid ratio 57, 62, 71, 390, 605
Monozeuxis 202
MORGAN, L. V. 276, *279*, 490, 498 *502*, 506 507
MORGAN, T. H. *56*, 277, *279*, 280, *293*, 348, *351*, 457, *465*, 484 491, 493, 498, 499, *502*, 504, 509, 512, *530*, 532, *583*, 585, *589*
Morphological changes 478
Morphological difference 195
Mortality 60
Complementary class 48
Morus 267
Mosaic, germinal 349
Mosaic in guinea pig *333*, **345, 347**
Mosaic pattern, agouti 336
Mosaic pericarp 372
Mosaics, somatic in guinea pig 350
Mosses 267, 276
MULLER, H. J. *56*, *72*, 348, *351*, 485, 489, *502*, *589*
Muller's hypothesis, balanced lethals 68, 71
Multiple allelomorphs *372*
Multiple factors, evidence with 327
Multiple stocks
Viability of 43
"Xple" 41
Multipolar spindle 135, 143
MURNAGHAN, F. D. 538, *583*
MURRAY 300
Mus 456
*decumanus*
*norvegicus* 456
*rattus* 456
*rattus alexandrinus* 456, 458
*rattus* color variability 457
*rattus rattus* 456, 458, 461
*rattus rattus* var. *brookei* 459
Mutant 503
Mutant characters 43, 250
Mutants, *Oenothera Lamarckiana* 231
Mutation 203–205, 345
Bud 348
Frequency 372
In Habrobracon 305
Somatic 348
To dominant allelomorph 341
Transplantable neoplasms 294
Mutational mosaic coat patterns of guinea pig 333
NABOURS, R. K. 5, *27*
NADLER, J. E. 584
NÄGELI, C. 178, *199*
NANJI, D. 178, 193, 194, *198*
Natural selection 533
Neoplasm 295
Neoplasms, mutations within 294
NICHOLS, G. E. *603*
Nicotiana 354, 451, 600
*Nicotiana alata* 466
*forgetiana* 466
*Langsdorffii* 466
*Sanderae* 476
Self-sterile 467
NIXON, CLARA 124, *126*
Nomenclature, committee on genetic forms and 214
Non-disjunction 484
NORTHROP, J. H. 584, *589*
NORTON, J. B. S. *402*
Norway rat 456
Nuclear changes
Meiosis **269, 273**
Prophase of meiosis 270, 272
Nucleolus 128, 129, 132, 135, 143, 144, 158
Nucleus, genes in 350
Numerical results of selection 531
NUTTALL, G. H. F. 73, 77, *82*
Oenothera **201,** 267, 276, 277, 354, 451, 601
*aurata*×*sulfurea* 224
*aurata*×*velaurea* 223
*aurata*×yellow 223
Backcrosses
Diheterozygote to double recessive 229
Diheterozygous yellow to old gold 218
Diheterozygous yellow to sulfur 218
Heterozygotes to recessives 211
*biennis* 138, 212, 232, 233
Genetic composition of 148
Heterotypic metaphase 140
Permanently heterozygous species 159
*biennis sulfurea* 138, 157, 212
Meiosis 127

Oenothera (continued)
*blandina* 147, 233
*brevistylis* 62 65 202
*brevistylis*×*Lamarckiana* 65
*decipiens vetaurea* 217
Deficiency *nanella-brevistylis* 60
*deserens* 147
Flower color 213
Flower-types 216
*franciscana* 128, 144 212
*franciscana sulfurea* 128, 138, 144, 146, 217, 221, 225
*gigas* 600
Gold center 215, 222
Origin 214
Recessive to all other colors 222
Segregates from sulfur crosses 224
Segregating *aurata* 215
Selfed 223
Homozygous
Old-gold 214
Sulfur 214
*sulfurea* 213
*sulfurea*×*aurata* 224
*vetaurea* 213
*vetaurea* and *sulfurea* 222
*vetaurea*×*aurata* 223
Yellow and old-gold 207
Yellow and *vetaurea* 209
Yellow×*aurata* 223
Yellow, formula of 214
Independence, old-gold 227
*Lamarckiana* 212, 231, 232, 233, 600
Hypothesis of mutation 69
Mutants from 231
Yellow×*vetaurea* 203
Zygote lethals of 217
*Lamarckiana vetaurea* 221
Meiosis in 145
*nanella-brevistylis*, segregation from crosses 57
*Nanella*, *rubricalyx* 226
Old-gold
Backcrosses of diheterozygous yellow 218
*brevistylis* independence of 227
Complementary to sulfur 212
Factor, independence of 226
Families derived from crosses 207
Flower color 201, 203
Formula of homozygous 214
Origin 203
Recessive to yellow 205
Sulfur-flower segregates 221
Type, probable differentiation 208
Origin of gold-center 214
*rubricalyx*, independence of *vetaurea* factor 227
*rubricalyx nanella* 226
*rubrinervis* 233
Second case of independent inheritance 201
*suaveolens* 212
Sulfur
Backcrosses of diheterozygous yellow to 218
Flowered segregates 221
Formula of homozygous 214

Oenothera (continued)
Old-gold complementary to 212
*sulfurea*
and *vetaurea* 222
Crosses of *aurata* to homozygous 224
Factor 157
×*Oenothera vetaurea* 213, 217
*vetaurea* factor independent of 227
Typical dihybrid ratios in 225
Yellow×old-gold 207
Olbrycht T. M. 41, 48
*Olea europaea* 75, 80
Oleaceae 75
Olive 75, 80
Olympia, Wash. 513
Ommatidia 506
Onslow, H. 189, *199*
Orange 74
Order of loci 260
Orientation spindles in anther loculi 268
Origin of chromosome incompatibility 148
*Oryza sativa* 191
Ovules, triploid 274
Oxidase 189
Pairing
Homologous chromosomes 138, 155
Threads 269
*Panicum miliaceum* 191
Papaver 601
*Paramaecium aurelia* 584
Parasynapsis 132, 145, 269, 276, 277
Parasynapsis *versus* telosynapsis 267
Parientales 74
Parnell, F. R. 411, *422*
Patterson, J. T. 457, *465*
Payne, F. *27*
Peach 74, 493
Pear 74, 80
Pearson, K. 394, 533, *583*
Pedigree, lethal 497
Pellew, C. 483, *502*
Percentage
Abnormal flies 285
Dominant individuals 574
Germinati on 59
Recombinations 41
Viable seeds 64
Percival, John 327, 329, *332*
Pericarp, variegation patterns in maize 372
Petersen, N. F. 38, *40* 407, *422*, 445, *455*
Phenotypes, gametic series 236
Phenotypic series 236, 239
Philipschenko, J. 583
Phillips, J C. 348, 349, *351*
Physiological difference, susceptibility and non-susceptibility 297
Physiology of egg production 123
Phytoprecipitins 73
Piebald, genes for 333
Pigeon, red 356
Pigment
Black 357
Depends on genes 350
Extension of melanic 358
Formation 189
Relation between enzymes 189

Pigment (continued)
Granules 356
Melanin 190
Production 190
Reactions attending 190
Plant, tetraploid 275
Plants, serodiagnostic researches in 79
Plasma 484
Plates, dorso-lateral 489
PLOUGH, H. H. 4, *27*, 44, *56*
Plum 74
Plumage color 355
Plymouth Rock 90
Pole 146, 147, 150
Affinity for 159
Attraction between chromosome and 160
Pollen 166, 325, 475
Carbohydrate reserves 163
Composition 166, 170
Lethal 228
Maize 38
Mother cell 127, 272
Reserve material 170
Reserves 39
Segregation, waxy×starchy maize 410
Starch 177, 196
Hydrolysis 184
Starch grains 175
Types, distinguishing 408
Pollen grains 326
Heterozygous plant 409
Maize 38
Pollen tube 435
Compatible unions 467
Factors 449
Growth 63, 64, 65, 71, 420, 436, 444, 451, 466, 468
Selective 475
Growth curve 475
Growth, incompatible 475
Growth rate of 70
Pollination, young bud 468
Pollinations, mixed 443
Polygalaceae 74
Polygenic character 257
Polygonaceae 75
Polyhybrid 534, 542, 556, 557, 561, 563, 567
Polyhybrid stocks 574
Polyhybrids, numerical results of selection 531
Polymerization 195
Polymerized amylopectin 194
Polymerized amylose 194
Polyploidy 317
Fragaria species 597
Polysaccharides, hydrolysis of 167
Pomaceae 79
Precipitin reaction in 79
Relation to the Prunoideae 79
Pomoidae 74, 80
Population 531, 532
Potato 75
Precipitin reaction 73, 74 77, 79, 81
Grafting 73
Modification 78
Preparation of extract 75
Prunoideae and Pomaceae 79
Pre-diakinesis stage, pollen mother cell 272
Presence-and-absence hypothesis 165
PREUSS, A. 74, 76, *82*
PRICE, H. L. 388, 393, *402*
Primrose, evening 201
Primula 441, 600
PRINGSHEIM, H. 193, *199*
Production, tumors 255
Progenies, defficiency in 211
Progenies, segregating endosperm generation 424
Progeny, gametophytic 83
Prophase 128, 323
Prophases, meiosis nuclear changes 270, 272
Proportions of zygotes 556
Proteins
Specific 73
Stereoisomeric forms of 79
Prunoideae 79, 80
Precipitin reaction in 79
Relation to the Pomaceae 79
Relationship of 79
*Prunus armeniaca* 74
*Prunus domestica* 74
*Prunus persica* 74
Pupation 489
*Pyrus communis* 74
*Pyrus malus* 74
QUACKENBUSH, L. S. 490, *502*
Quince 80
Rabbit 532
Blue varieties 465
Radiating loops 133
RAEDER, F. 74, *82*
RALSTON, R. 91, 126
Ranales 74
Rat 5, 456, 532
Agouti 463
Black 456, 458, 459, 463
Black recessive 457
Blue 459, 463
Chocolate 457
Cinnamon type 457
Cream 459, 463
Roof 458, 463
Wild black 463
Yellow 457
Rate, pollen tube growth 429, 430, 440, 449, 467
Ratio
Color segregation 448
Complementary classes 49
Gametes at fertilization 441
Monohybrid 57, 71
Waxy endosperm 427
Reaction
Host and tumor 301
Transplantable tumor cell 302
Recessive
Backcrossed to heterozygotes 211
Deficiency of 211
Percentages of 440
Recessive type, inferior 225
Reciprocal crosses 479, 491
Recombination of tumor 262
Recombination percentage 41, 45

REDFIELD, HELEN **482,** *502,* 507, 508
Reduction division **320,** 324
REE, E. *602*
REICHERT, E. T. 79, *82*
RENNER, O. 148, 151, *162*
Repulsion phase 227, 237, 238, 240, 241
Reserve carbohydrate 196
Reserve material, waxy endosperm 169, 170, 181
Residues, early growth 186
Residues linked 195
Residues, number of hexose 195
Reticulate condition, return of chromosomes to 144
Reticulum 144
*Rheum officinale* 75, 80
Rhode Island Red 90, 124
Rhubarb 75, 80
Rice
  Glutinous×ordinary 411
  Starch 194
Rice Pop 433, 442
RICHARDSON, C. W. *603*
RICKETT, H. W. 85
RIDGWAY, R. 39, *40,* 457, *465*
Ridgway's standards 39
ROBERTS, E. 4, *27,* 584, *589*
Rosa 597, 601
Rosaceae 74
ROSENBERG, O. 597, 600, 601, *603*
Roughoid 258, 260, 493
ROUX, E. 178, *199*
Rubus 597
RUEHLE, K. 79, *82*
Rutaceae 74
RYDBERG, P. A. 591, *603*
Rye, **317,** 319
  Anaphase 320
  Chromosomes 317, 320
  Metaphase 320
  Petkus 319
SAKAMURA, T. 597, *603*
Salivary amylase, hydrolysis with 182, 184
SALTZMANN, B. 74, 75, *82*
SAMEC, M. 194, *199*
Sampling, fluctuations 12
Sarcophaga 276
SATO, S. 192, *199*
SAX, H. J. *332*
SAX, K. 297, 317, 322, 327, 328, 329, *332,* 601, *603*
Secondary maxima, tendency for occurrence of 120
Second-chromosome 503
Second-chromosome tumor gene, locus 261
Seed
  Composition 166
  Failure to germinate 237
  Fertility 59, 60, 68
  Forced germination 58
  Malnutrition 58, 65
  Per capsule 64
  Percentage viability 64
  Residues 186
  Viability 58
Seedling development, digestion of endosperm reserves 184
  Growth 185–187
Segregate, double-recessive 214, 222
Segregating progenies 425
  From high defective ear 426, 428
Segregation 38, **57,** 385
  Both parents heterozygous 414
  Carbohydrates 407
  Endosperm 411
  Following self-fertilization 229
  Gold-center from its crosses with sulfur 224
  Pollen 411
  Selfed parental plants 450
  Short-style complex 67, 71, 72
  Short-styled plants 62
  Upper and lower halves of ears 429
  Waxy and starchy grains 409
Selection 370, 488, **531**
  Effects of 572
  Male 370
  Polyhybrids, numerical results 531
Selective
  Action 435, 436, 445
  Fertilization 247, 451, 474
  Maize 443
  Mating 532, 572
  Pollen stimulation, hypothesis 474
  Pollen tube growth 475
Self-fertilization 222, 229
  Segregates 222
  Segregations following 229
Self-sterility 466
Semi-lethal character 428
Separation
  Chromosomal 138
  Regular 138
Sequence, chromosomes in 159
Seriation of stages 268
Serodiagnostic researches in plants 79
Sex chromosome, Drosophila 440
Sex, maize 15
Sex-count 485
Sex-limited lethal **482,** 489
Sex-linked gene 358
Sex-linked lethal 486, 489
Sex-ratio 485, 487, 490, 499
SHAFFER, P. A. 167, *199*
SHARP, L. W. 144, *162,* 269, *279*
Shell 500
SHERMAN, H. C. 178, 192, 194, *199*
Shifting of gametes 565, 576
Short-style complex 58, 59, 67, 71, 72
Short-styled plants 62, 64
  Segregates 71
SHULL, G. H. 58, 71, *72,* **201,** 212, *234*
Silkworm moth, egg characters 483
Silver King 167
Ski 249
Skins, color types of 460
Smears in iron-acetocarmine 319
Solanaceae 75, 80
*Solanum lycopersicum* 267
  *Tuberosum* 75
SOLIMUS-LAUBACH *603*

Somatic
Metaphase, triploid 272
Mutations 348
Tumor cell 301
*Sorghum vulgare glutinosum* 191
Species hybrids 328, **600**
Specific proteins 73
Speltoid mutation 328
Sperm lethal 154, 221
Sphaerocarpos, gametophytic inheritance 83
Spindle
Anther loculi, orientation 269
Bipolar 138
Homeotypic 143
Multipolar 135, 143
Spineless 493
Spireme **129,** 133, 157, 274
Alternation of threads 274
In circle 133
Open 129
Paired and unpaired threads 274
True 269
Spontaneous neoplasm 295
Spore tetrads 85
Sporophyte, Mendelian ratios 453
Squirrel Tooth 433
STADLER, L. J. 1
Stages, seriation 268
Staining, carbohydrates in endosperm 409
Standard map 55
Standards, Ridgway's 39
Starch 38, 169
Amylose in endosperm 179
Arrowroot 194
Barley 194
Color reactions, iodine 177
Determinations 169
Diploid tissue 408
Endosperm 177
Pollen **177,** 196
Preparation 171
Preparation of pure form, 171
Rice, 194
Waxy maize 168, 192
Wheat 194
Starch grains 171
Composition of 178
Form of 171
Maize 175
Pollen 175
Starch hydrolysis 181–184
Starch molecule, structure 193
Starchy carbohydrates 408
Starchy kernels, physical appearance 409
Starchy pollen, carbohydrate reserve 420
STARK, M. B. **249,** *266*
STEINECKE, F. 74, *82*
Stereoisomeric forms, proteins and carbohydrates 79
Sterile seeds 61, 62
Sterility **466,** 488, 530
Both sexes 488
Correlated 489
Sterility group 479
Sterilization, fractional 76
STERN, CURT **503,** 504, 510, 511, 513, 515
Stigmas 468
Stippling 369
STOMPS, T. J. *162*, 212, *234*
Strawberry 590
Strepsinema 133
STRONG, L. C. **294**, 296, *303*
Structure of the starch molecule 193
Struggle for existence 65
Stumpy seedlings 63
STURTEVANT, A. H. *27*, *56*, 277, *279*, 280, *293*, 348, *351*, 483, 490, 501, *502*, 509, 512, *530*, 585, *589*
Sugar, maize 168
Survey, cells in heterotypic metaphase 140
Susceptible individuals 295
Susceptible mice, ratio 297
SVENSON, H. K. *27*
SVENSON, J. K. 4, *27*
Swedish wild stock 280
Synaptic conjugation 129
Evidence of 129
Synizesis 128, 269
Synizetic knot 129
Synzeuxis 202
TÄCKHOLM, G. 597, 601, *603*
TADOKORO, T. 192, *199*
TAHARA, M. 597, *603*
TANAKA, Y. 192, *199*, 483
Telophase 142
Telosnyapsis 144, 267, 277
Temperature **283, 284, 584**
During pupation 489
Effect 4
Effect on crip-h flies 203
Effect on length of wing 584
Unfavorable to algae 84
Variations 467
Teosinte 411
Testis, guinea pig 340
Tetrads 326
Pollen 325
Spore 85
Tetrahybrid 560
Tetraploid 317
Fertilized by diploid germ cell 275
Plant 275
Theory
Adaption 300
Virulence 300
Third chromosome 255
Main gene for tumor 257
Recessives, effect on tumors 250
Tumor gene, locus of the main 258
THOMPSON 489
THOMPSON, W. C. 89
THOMPSON, W. P. 317
Threads, longitudinal pairing of 269
Time, growth of pollen 64
Tissue
Endosperm 408
Specificity 297
Tomato 75, **267**
Albino 389
Chromosome number of normal diploid 269
Chromosomes in pollen mother cells 353

Tomato (continued)
Diakinesis 353
Dihybrid and polyhybrid 391
Diploid 267
Dwarf Aristocrat 352
Dwarf Champion 354
Flesh color 389
Foliage color 389
Fruit shape 388, 389
Globe 353
Independent assortment 394
Independent inheritance 402–405
Inflorescence 389
Leaf shape 389
Linkage **387**, 392, 394–396, 398–400
Color of flesh 400
Color of foliage 400
Color of skin 400
Crossover 393
Crossover value 392
Dwarf Aristocrat 392, 393
Flesh color 394, 396, 397, 398
Foliage color 396, 397, 400, 401
Fruit contour 395, 398, 399, 401
Fruit neck constriction 397
Fruit skin color 395, 398, 399
Genetic relations of 394, 396–399
Grape cluster 393
Group 391
Leaf shape 395, 397, 398, 401
Nine pairs of genes in six groups 401
Pink peach 392
Pubescence of fruit skin 396
Skin color 396, 397
Stature 394, 395
Yellow pear 392
Maturation processes 268
Ponderosa 389
Repulsion 392
Skin structure 388
Triploid **267**, 352
Trisomic inheritance of dwarf 352
Trisomic plants 353, 354
Unifactorial nature of characters 390
Vine habit 388
TOYAMA, 483
Transplantable
Neoplasms, mutations within 294
Tissue, host's tolerance of 294, 301
Transplantation 299
Malignant tumors 300
Tri-amylose 194
Trihybrid **539, 559**
Triploid
Configurations 274
Early meiotic prophase of 267
Maturation in 273
Method of origin 275
Tomatoes 267, 352, 367
Viable ovules in 274
Triploidy 267
Trisomes, early diakinesis 272
Trisomic set, crossing over between members of 267
Triticum 597, 601
*dicoccum* 328
Triticum (continued)
*durum* 328
*monococcum*×*turgidum* 601
*polonicum*×*spelta* 601
*vulgare* 318, 320, 328
*vulgare*, hexaploid 327
TSCHERMAK, E. VON 329, *332*
Tumor **249**, 261, 296–298
Backcross 264
Borne by star and dichaete flies 250
Cell, internal change in genetic constitution 301
Reaction between host 294
Reaction potential 302
Somatic mutations 301
Crossing over decreases production 255
Drosophila 249
Linkage relations 249
Gene, locus 262
Second chromosome 261
Third-chromosome 250, 258
Host's tolerance of transplantable 301
In bar flies 264
Inheritance of susceptibility 294
Main gene in third chromosome 257
Mass deviates from parental genetic constitution 302
Order of loci 260
Parentage 261
Polygenic character 257
Produced by third-chromosome recessives 250
Reaction potential between host 301
Recombination 262
Star and dichaete flies 250, **254**
Stock, roughoid 258
Tissue 294
Fate of implanted 294
Transplantation of malignant 300
TURPIN, G. 91, *126*
Twin megaspore mother cells 271
TYZZER, E. E. 296, *303*
UDA 483
UHLENHUTH, P. 73, 77, *82*
Univalent chromosomes, closed circles 158
Failure of halves to move to opposite ends 322
Splitting 322
United States Department of Agriculture 590
University of Maine 309
Uvularia 267
VALLEAU, W. D. *604*
Variability 281
Coefficient 7
Crossing over 5
Crossing over in maize 1
Crossover percentage **7, 8, 10, 11**
Variation
Tumor 297
Crossing over **3, 15, 16**
Female percentage 488
Intra-clonal 86
Variegation 373
Maize 372
Vermilion 485

Viability
  Differential 49, 247
  Gametes 237
  Pollen 420
Vineland international egg laying and breeding contest 90
Viola, 597
Virulence, theory of 300
Vortex, complex inheritance 249
VRIES, H. DE 57, 58, 66, 69, *72*, 127, 149, *162*, 202, 212, 231 *234*, *354*
WACHTER, W. L. 5, *26*
Waltzing 457
WARD, L. 44, *56*, 493, 507, *530*
WARNER, D. E. 89, *126*
WARREN, H. C. 484, 533, 577, *583*
WARREN, P. A. 388, 389, *402*
WASSERMANN, A. 73, 77, *82*
WATKINS, A. E. 331, *332*
WEATHERWAX, PAUL 7, *27*, 165, 166, 191 191, *199*, 407, *422*, 445, *455*
WENE, E. H. 91, *126*
WENTZ, J. B. 420, *422*, 442, *455*
WETTSTEIN, F. 452, *455*, 585
Wheat 317, 597
  Anaphase 320
  Characters 319
  Chromosomes 320
  Emmer types 328
  Hybrids 322
  Hybrids, bivalents 327
  Metaphase 320
  Parent, back-crossing with 327
  Starch 194
WHELDALE, M. 188, *199*
White Leghorn 89, 90, 124, 125
White Wyandotte 90, 124
WHITING, A. R. 305, 307, *316*
WHITING, P. W. 305, 306, 307, 309, *316*
WILSON, E. B. 277, *279*
Wing, stunting 489
WINGE, O. 327, *332*
WINKLER, H. 269, 275, 276, 278, *279*, 387. *402*
WOGLAM, W. H. 300, *303*
WOODRUFF, L. L. 584, *589*
WOODWORTH, C. M. 235, *248*
WRIGHT, S. 189, 190, *199*, 333, *351*, 532, 533, *583*
X-chromosome 485, 498, 501
  Crossing over 54
  Maps 54
Xple 41, 43
Xple, alternated backcross 50
X-rays 4
Y-chromosome 498
YASUI, K. 601, *604*
Yellow 498
Yellow mice 451
*Zea mays* 1, 433
ZIEGENSPECK, H. 80, *82*
ZIRKLE, CONWAY 531
Zygote 1
  Death of female 482
  Dies 499
  Dominant 536
  Lethals 72, 217, 448
  Malnutrition of 71
Zygotic generations 534

C30